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Intensive tool-practice and skillfulness facilitate the extension of body representations in humans

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ABSTRACT

The brain's representation of the body can be extended to include objects that are not originally part of the body. Various studies have found both extremely rapid extensions that occur as soon as an object is held, as well as extremely slow extensions that require weeks of training. Due to species and methodological differences, it is unclear whether the studies were probing different representations, or revealing multiple aspects of the same representation. Here, we present evidence that objects (cotton balls) held by a tool (chopsticks) are rapidly integrated into the body representation, as indexed by fading of the cotton balls (or 'second-order extensions') from a positive afterimage. Skillfulness with chopsticks was predictive of more rapid integration of the second-order cotton balls held by this tool. We also found that extensive training over a period of weeks augmented the level of integration. Together, our findings demonstrate integration of second-order objects held by tools, and reveal that the body representation probed by positive afterimages is subject to both rapid and slow processes of adaptive change.

1. Introduction

Imagine a skillful tennis player immersed in a heated match requiring his upmost capacity and focus. For an external observer, the tennis player is typically considered an independent actor and cause of the events he initiates within his surrounding environment. But in the tennis-player's mental experience, his body, the racket and even the ball can be felt as part of his sensory and intentional self. As the ball approaches, his thoughts are less likely to be on the desired trajectory of his arm, than on the trajectory of the racket head. When the racket makes contact with the ball, the feeling of impact is perceived not at the tactile sensors in his hand, but in the racket head itself. At high levels of skill and concentration, even the racket may become secondary in his experience, all thoughts becoming based on the ball and its desired trajectory. This ability for conscious awareness to be focused on the ball requires that the intermediate effectors (muscles, joints, racket) be integrated into a subconscious, automatically processed model. This model must be capable of tracking the current states of the effectors, and of back-calculating conscious goals into basic motor commands.

The original positing of a model representing the body came from studies of neurological patients by Head and Holmes (1911). Based on observed deficits in postural awareness and tactile localization, they proposed that the normally functioning brain has two types of bodily representations. First there is the *body image*, a conscious representation that is the subject of our thoughts and perceptual judgments. Second, there is the *body schema*, an unconscious framework that automatically integrates posture, proprioceptive input and action goals into a common spatial frame.

The *body image* is believed to be a multisensory representation of the body that integrates stored knowledge, and by subserving mainly perceptual purposes it is subject to bodily illusions (Kammers, Kootker, Hogendoorn, & Dijkerman, 2010). For example, vibrations applied to a tendon causing the sensation of that tendon stretching will result in the perceptual experience of the corresponding limb being moved (Goodwin, McCloskey, & Matthews, 1972). Another manipulation of the body image is demonstrated by the 'rubber hand illusion'. Here, sensory conflict is induced by simultaneous stroking of the own (unseen) hand and

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a visible rubber hand, resulting in an experience of tactile sensations occurring at the rubber hand (Botvinick & Cohen, 1998).

The *body schema*, on the other hand, is described as an unconscious representation that subserves action rather than perception. Head and Holmes proposed that this schema does not exclusively code for the physical body, but is capable of extending to objects that are needed to support skilled actions or smooth movement through the environment. Thus, the body schema would need to include tools, or even a large feather in one's hat, in order to support one's actions or avoid collisions. Though generally believed to be highly robust, also this motoric body representation is not entirely immune to bodily illusions. For example, after inducing the rubber hand illusion, the grip aperture of a real hand was found to mimic that of a rubber hand (Kammers et al., 2010).

Since the early work of Head and Holmes, people largely agree on the existence of multiple body representations, though their exact number and definition is still a matter of debate (Cardinali et al., 2009, 2012; de Vignemont, 2010; Kammers, et al., 2010).

Evidence that tools become integrated into these body representations has come via various experimental routes. Changes in the *body schema* are most directly observed by monitoring the kinematics of action execution. In a study by Cardinali et al. (2009), participants who used a mechanical grabber subsequently changed the kinematics of their empty-handed movements, pointing and grasping as if their arms had lengthened. Simple motor learning was an unlikely account for these changes, as the kinematics of tool-use itself did not change throughout the period in which the mechanical grabber was used. Given that tool-use induced changes in empty-handed actions, the results suggested that a change had occurred in a generalized model of action generation. These findings therefore imply a highly plastic representation of the body schema, similar to what had been suggested by Head and Holmes almost a century prior.

The other major class of tool-use experiments uses measures of multimodal integration to investigate body representations (Maravita & Iriki, 2004). Certain sensory processes are selective for stimuli originating from within “peripersonal space”, which corresponds to the reachable or “actionable” space immediately surrounding the body. Bodily representations both define the extent of this space, and also form a basis for the spatial mapping of sensory stimuli within it. Thus, monitoring changes in the extent and organization of this sensory space allows one to infer changes in body representations.

A lot of what is known about body representations in peripersonal space comes from neurophysiological studies in primates. Fronto-parietal networks have been identified that continuously update spatial representations of body shape and posture. These networks integrate multimodal sensory information (primarily proprioceptive, somatosensory and visual information) such that it is functionally relevant to specific actions, and serves the ability to localize the body in space (Colby, 1998; Maravita, Spence, & Driver, 2003; Rizzolatti, Fadiga, Fogassi, & Gallese, 1997). Notably, there are neurons in ventral-premotor cortex that have both somatosensory and visual receptive fields, coding for the space surrounding the same body part. These bimodal neurons integrate information such that even if a body part (for example a hand) is moved through space, the visual receptive field remains anchored to the body part it belongs to Graziano, Yap, and Gross (1994).

Intriguingly, these fronto-parietal networks can represent external objects in a similar fashion. After weeks of practice with a simple tool, bimodal neurons in intraparietal cortex of macaques were found to expand their visual receptive fields to include the space surrounding the tool whenever the monkey was engaged in deliberate tool interaction (Iriki, Tanaka, & Iwamura, 1996). This finding suggests that peripersonal space can be expanded via the use of a tool (but see also Holmes (2012)). Similarly, a study investigating structural brain changes in macaques exposed to tool-use training for the first time, showed an increase in grey matter volume in fronto-parietal areas including intraparietal cortex (Quallo et al., 2009). In a study of a human patient with right-hemisphere lesions, tool-use altered the domain in which visual neglect was experienced. Whereas the patient's visual neglect was typically restricted to judgments regarding stimuli in peripersonal space, the neglect spread to more distant areas if the task was performed using a long pointing tool, again suggestive of the expansion of peripersonal space (Berti & Frassinetti, 2000). Increased multisensory weights assigned to the processing of visual stimuli around the *functional* part of a tool are likely responsible for the remapping of peripersonal space to include this new region of space after tool-use (Holmes, 2012). Note that none of these studies probed motor output as a dependent measure, so it is unclear whether these body representations subserve action planning as a body schema, or if they subserve only perceptual processing.

The present study utilizes another method of probing bodily representations, which has recently been extended to investigate tool use. The paradigm involves a cross-modal effect whereby proprioceptive inputs profoundly disrupt visual representations of the body (Bross, 2000; Davies, 1973a; Gregory, Wallace, & Campbell, 1959). In these experiments, participants in a completely darkened room are exposed to a brief flash of light, which creates a crisp, long-lasting afterimage of the entire field of view. When the afterimage includes a body part, such as the participant's arm, moving the arm from its imaged position causes the afterimage of the arm to ‘fade’ or ‘crumble’ while the rest of the afterimage scene remains intact. The mismatch between proprioceptive and visual representations of the same body part leads to a Gestalt-like disruption of the visual percept. Versions of this experiment done with mirrors confirm that this fading effect occurs in accordance with proprioceptive and visual representations organized on the basis of one’s own body (Ritchie & Carlson, 2010).

Such afterimage-based experiments have also demonstrated the rapid modulation of body representations to include held objects. Carlson, Alvarez, Wu and Verstraten (2010) showed that objects grasped by the observer (referred to as *‘first-order’ objects*) faded upon being dropped. Similarly, when the observer removed a first-order object from the area of peripersonal space being viewed in the afterimage, the object would also fade. This indicates that somatosensory and proprioceptive information is integrated with visual information in much the same way for both held objects and body parts.

Afterimage studies do not investigate motor output, and thus the body representations that were probed may or may not function as body schema. The representations seem more clearly akin to the ones probed in the studies of peripersonal space. Both involve multisensory integration and measurements based on perceptual outcomes. Using the afterimage paradigm, we aim to address several related issues raised by the preceding studies. What kinds of external objects are assimilated? What factors govern whether or not an object is assimilated? How quickly does assimilation occur?

Although the monkey physiology studies found that tool integration developed after weeks of use (Iriki et al., 1996), the human behavioral studies found tool integration as soon as the tools were grasped (Cardinali et al., 2009; Carlson et al., 2010). The behavioral findings closely match our daily functioning and the feeling that we can rapidly assimilate objects (like picking up a pen and beginning to write). There are many functional advantages to a body system capable of rapidly incorporating, as well as disincorporating, an object or tool. The ability to readily expand the physical body in a functional manner via tool-use enables us to do numerous things that would not otherwise be possible, such as removing hot coals from a fire or hitting a nail into a wall. Being able to readily disincorporate a tool after it is no longer used allows us to keep a coherent sense of the body's boundaries. Such short-lived changes in the brain's representation of the body might be most effectively established by flexibly updating representations of peripersonal space (Bruggeman, Kliman-Silver, Domini, & Song, 2013; Carlson et al., 2010; Holmes, 2012). However, extending the body into space for functional purposes could also involve updating of the action oriented body schema (Cardinali et al., 2009).

Such a flexible system could be beneficial for the incorporation of tools, but also for objects held by tools. Certainly we do many things involving second, or even higher order extensions. Extreme examples of this are operating construction vehicles, performing robotic surgery, etc. But there are also many more low-tech examples, such as the use of chopsticks to manipulate food while eating a meal. Taking this marked degree of flexibility, and the goal-oriented nature of tool-use and body representations into account, one could readily anticipate representations for higher-order extensions.

However, the afterimage experiments revealed complex results regarding second-order extensions. When participants used a simple, table-supported, mechanical arm that could grip objects when squeezing a handle, objects held by the tool did not fade from the afterimage when participants released the arm's handle (Bruggeman et al., 2013; Carlson et al., 2010). This finding demonstrates that an observer's ability to consciously predict the consequences of an action (e.g. a hand movement leading to release of an object) is not sufficient to induce fading of an object from the afterimage.

But in light of the sensitivity that the body's representation has for afferent sensory input (Carlson et al., 2010; Hogendoorn, Kammers, Carlson, & Verstraten, 2009) the apparent failure to integrate higher-order external objects seems counter to our daily experience. In fact, the study by Bruggeman et al. shows that second-order objects can also fade from the afterimage when released from a mechanical arm, as long as participants are able to freely wield the tool. Contrary to using a tool while it is fixed to a table, freely wielding the same tool offers rich somatosensory feedback, providing the information necessary to experience fading of a second-order object (Bruggeman et al., 2013).

The critical factor, Bruggeman et al. suggest, is that target objects can be perceived directly, or indirectly via a tool, through 'dynamic touch'. Dynamic touch can be defined by the combined muscular effort and sensory consequences of manipulating an object (Gibson, 1966; Yamamoto & Kitazawa, 2001). Mechanoreceptors in the hand are able to detect mechanical forces (such as torque, and moment of inertia) that emerge when one manipulates a tool, and such signals (mainly the inertia tensor) can be used by the brain to quantify for example the length of a handheld object without requiring vision (Turvey, 1996). Dynamically manipulating an object involves both perception and action, allowing the object to become incorporated into the action and somatosensory system (Bruggeman et al., 2013).

The importance of action is also demonstrated by studies where the simple physical presence of a tool does not induce remapping of peripersonal space, which instead requires deliberate tool-action (Farnè, Iriki, & Làdavas, 2005; Iriki et al., 1996; Wagman & Carello, 2001). Moreover, the ability to predict action outcomes is crucial for tool-use, and requires a tight link between motor predictions and feedback from the somatosensory system (Wolpert, Goodbody, & Husain, 1998; Wolpert & Flanagan, 2010). Thus, a flexible and quickly adaptive system consisting of a feedback loop between perception and action would be well suited to the demands of rapidly incorporating and disincorporating second-order objects and tools.

Given that (afterimage) studies in humans reveal a highly flexible and rapidly changing body representation, capable of assimilating even second-order objects, why do studies of macaque neurophysiology only reveal slowly changing representations? One explanation for this might be the existence of multiple representations that differ in learning speed, as proposed by Carlson et al. (2010). Alternatively, differences in assimilation speed of objects could be due to the amount of sensorimotor feedback provided by a given tool (Bruggeman et al., 2013). Finally, differing assimilation speeds found by various studies could stem from important differences between species. Whereas humans are dexterous tool-users, lower primates are not consistently known to engage in the spontaneous use of tools (Iriki et al., 1996; Tomasello & Call, 1997). It's been suggested that, in macaques, training is needed to activate silent neurogenetic mechanisms (Ishibashi et al., 2002b; Tomasello & Call, 1997), which represent a precursor of the tool-use abilities acquired by humans over the continued course of evolution (Ishibashi et al., 2002a). This could account for the slower buildup needed to find integration of external tools into the body representation of monkeys.

At present, studies in human subjects have not tested for changes in tool integration across the long timescales present in the monkey studies. Conceivably, long-term practice could improve somatosensory perception of a tool, leading to better predictions of motor actions performed with that tool. Such slowly evolving improvements in dynamic touch may drive neural plasticity during tool-use, changing the extent to which second-order objects are assimilated. This would reveal whether plasticity in the human body representation underlying the fading effect contains a slow component.

In the present study, we use the afterimage paradigm to investigate tool integration during the use of chopsticks. Chopsticks provide rich somatosensory feedback during use, and are thus a good choice where dynamic touch is important. We first verify the existence of second-order integration by using chopsticks. This is not entirely a given, since chopsticks rely more on finger representation and kinesthesia, while the long mechanical grabbers used in previous research are likely to rely on information from more proximal parts of the hand and arm representations (Bruggeman et al., 2013; Cardinali et al., 2009, 2012; Carlson et al., 2010).

Second, we test for both elements of rapid integration and build-up through training. In two successive experiments we assess whether skillfulness with a tool can modulate potential rapid integration, and whether extensive tool practice in humans can result in long-term integration processes, similar to that found in monkeys. Throughout, we compare participants' dominant and non-dominant hands, which provides within-subject control. Also, this helps us answer a third possible question, since the degree of life experience with a tool needed to modulate the fading effect is an open question–handedness covers one extreme, since it is built up over one's entire lifetime.

Here, we demonstrate that second-order objects do fade fairly frequently, validating the idea that space representations around the body can be modified to include second-order objects. We find that such integration of second-order objects includes both a rapid component, as well as a longer-term component that can be built up over the course of extensive training. These findings provide a link between the fast and highly flexible integration of objects found in many behavioral studies with humans, and the slower buildup of tool integration through training found in monkey studies.

2. Material and methods

2.1. Participants

Fifty-nine healthy volunteers were recruited from Maastricht University (35 female, 51 right-handed, mean age ~22 years). Data from eight participants were excluded due to missing audio-recordings ($n=1$), inability to hold chopsticks ($n=1$)

and failing a pre-experimental screening procedure (see below, $n=6$). Eight volunteers, including two of the authors (RR and IB) also participated in experiment 2: a four-week training and post-training assessment. All participants had normal or corrected-to-normal vision, agreed to the use of voice-recordings and provided written informed consent. Participants were reimbursed by means of course credit. The study took place under the approval of the standing ethical committee of the Psychology and Neuroscience department at Maastricht University.

2.2. Materials and procedure

Experiments were conducted in a completely darkened room. Participants were seated facing a table and wall covered by a black cloth (1.56 cd/m^2) extending ~60° of visual angle horizontally. Afterimages were created using a handheld Vivitar 285HV Zoom Thyristor flashgun directed at the ceiling. Participants' verbal reports were collected with an iRiver (iHP-120 multi-codec jukebox) device. Wooden chopsticks (24 cm in length, unfinished) were employed for all experimental operations: experimental trials, training and a skill test. The second-order objects were cotton balls dyed in black tea (88.3 cd/m^2), which were easily graspable with chopsticks and provided no auditory feedback when dropped.

Because our experiment depends on the ability of participants to experience object fading, we conducted a separate pre-experimental screening procedure assessing the ability of each participant to see changes in the positive afterimage in response to bodily movement (Carlson et al., 2010). Participants were excluded from further participation if no such changes were reported after six screening trials. Prior to the experiment, participants were instructed how to hold chopsticks (one pair in each hand) and were allowed a brief practice. We instructed participants to keep their elbows on the table in front of them, positioning their hands ~30 cm in front of their face and ~35 cm apart. Participants maintained stable fixation by steadily gazing at a point halfway between their hands. After instructions, participants were dark adapted for 10 min.

An experimental trial (Fig. 1) started with participants using the chopsticks in each hand to pick up two cotton balls. A flash was emitted and participants verbally indicated the start of their afterimage, whereafter they dropped one of the two cotton balls. Participants described any perceived differences between the two sides: the Action Side from which the object was dropped versus the Stationary Side where nothing was dropped. To provide a measure of overall afterimage duration, participants indicated when the entire afterimage had faded back to complete darkness. After each trial participants had to pick the cotton balls back up in preparation for the following trial. In order to accomplish this we used a red laser pointer to help participants get their bearings in the dark. Since the wavelength of red light falls outside of the sensitivity range for retinal rods, this was a useful way to prepare for upcoming trials without disturbing dark adaptation.

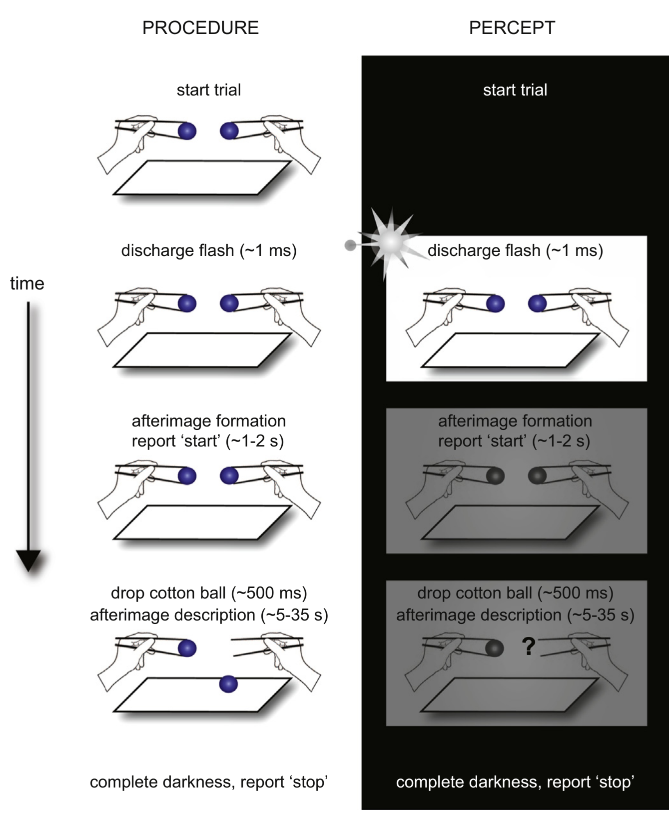

Fig. 1. Trial sequence. An experimental trial began with participants sitting in complete darkness while holding a pair of chopsticks in each hand, and a cotton ball between each pair of chopsticks. After discharge of a flash, participants were instructed to drop a cotton ball upon formation of the afterimage from either the dominant or the non-dominant hand. Participants then described any perceived differences between the objects in the afterimage, comparing the Action Side (where the cotton ball was dropped) with the Stationary Side (where the cotton ball was stationary).

Each participant performed 20 trials: a cotton ball was dropped from the chopsticks in the dominant and the non-dominant hand 10 times each, switching sides every 5 trials (counterbalanced across participants).

After completion of the experimental trials, participants performed a skill test with chopsticks using their dominant hand. During part A (3 trials), participants moved 10 small, curved objects (uncooked macaroni, 8 mm in length) from one cup into another (diameter=8.4 cm; height=5.85 cm) over a distance of 20 cm. During part B (3 trials), participants moved 5 small square objects (standard dice, 15-mm cubes) over a distance of 20 cm, stacking them on top of each other. Direction of movement (left-to-right or right-to-left) was counterbalanced across trials, and the order of the two parts was counterbalanced across participants. We assume that faster performance indicates higher degree of skill, allowing the average trial duration to represent a measure of chopstick-skill. However, the ecological validity of part B was questionable, since it contained a spatial component and was prone to catastrophic errors in cases where the stacked objects would tip over. This is reflected in the large variability of performance on part B (mean=43.44 s; $SEM=5.58$ s) compared to part A (mean=49.09 s; $SEM=2.74$ s). Since it wasn't possible to evaluate post-hoc which trials had involved catastrophic error(s), and to avoid classifying many participants as outliers, participant's chopstick proficiency was defined as the average trial duration on part A of our skill test. After outlier removal (99.3 coverage, $sd \approx 2.7$, removed $N=1$), average trial completion time was 47.75 s ($SEM=2.44$). Note that the main results of the research presented here are identical whether skill is defined based on the full test, or on part A alone.

After completing experiment 1, eight participants continued with chopstick training in a naturalistic setting. For a period of 4 weeks they ate at least one meal per day with chopsticks, using their dominant hand (15–28 meals per participant, mean=23.5 meals). Participants were tested again after training, exactly as in Experiment 1. Since training exclusively targeted the dominant hand, the non-dominant, non-trained hand served as a within-subject control.

2.3. Analyses

Reports on the appearance of objects in afterimages can vary widely between individuals (Davies, 1973a, 1973b). In this study, responses ranged from 'no perceived differences' to 'premature fading', 'transparent dimming', or even complete disappearance of one or several objects in the afterimage. We categorized responses as in Carlson et al. (2010), labeling reports (based on descriptions of the second-order objects) indicating greater fading on the Action Side vs. Stationary Side as positive responses. Two independent observers blindly rated every voice recording collected.

Due to the binary nature of our outcome measure (fading vs. no fading), and difficulties associated with modelling probability which has a restricted range of 0–1, we analyzed the data using logistic regression models in Stata (StataCorp., 2009). Specifically, we used a logistic random-intercept model, which allows fitting individual intercepts to participant's data to account for inter-individual differences in baseline fading experiences. Interactions were interpreted using simple slope analyses. In Experiment 1, skill was modeled as a continuous between-subjects variable, and the hand used to perform the action was modeled as a categorical within-subjects variable. In Experiment 2 both training and hand were modeled as categorical within-subject variables.

3. Results

3.1. Experiment 1: Second-order fading, skill and lifetime-built motor fluency

Second-order integration, as indicated by fading of a cotton ball held with chopsticks from the Action Side was experienced on 26% of experimental trials ($t=9.762$; $p<0.0001$, one-sided against zero). This finding uncovers the ability of human observers to rapidly integrate the chopsticks into the body representation, with the chopsticks providing rich cross-modal expectations about the effects of dropping the second-order cotton ball.

With regard to handedness, we find that at a mean skill level, the odds of experiencing fading are 46.4% higher when the cotton ball is dropped from the chopsticks in the dominant, as opposed to the non-dominant hand (exp(B)=0.381; $p=0.025$). Moreover, our data also revealed an interaction between hand and skill (exp(B) = −0.031; $p = 0.004$). As depicted in Fig. 2a, when dropping the cotton ball from the chopsticks in the non-dominant hand, skill level did not influence the amount of fading participants experienced (exp(B) = 0.001; $p = 0.948$). However, when using the dominant hand, more skilled (faster) participants perceived more fading of the cotton balls (larger log odds) than those participants whose skill with chopsticks was poorer. In fact, the odds of experiencing a cotton ball fading increased 0.03% for every second a participant was faster on the chopstick-skill test (exp(B) = −0.029; $p = 0.035$). The model provided a good fit for the data (Wald Chi-Square(3) = 16.33; $p = 0.001$).

Note that the results depicted in Fig. 2 are expressed in log odds of fading. The relationship between log odds and probability can be defined as:

$$\text{log odds}(p) = \log\left(\frac{p}{(-p)}\right)$$

where p stands for the probability of fading. As a reference, log odds of zero correspond to a 50% chance of perceived fading, whereas log odds smaller than zero indicate a chance of fading which is less than 50%.

Afterimage durations were not affected by our experimental manipulations. Linear regression revealed no relationship between skill and duration of the afterimage (dominant hand: $R^2 < 0.0001$; slope = 0.001 with 95% CI = [−0.099–0.101]. Non-dominant hand: $R^2 = 0.005$; slope = −0.024 with 95% CI = [−0.125–0.077]). Moreover, afterimages were of similar durations regardless of the hand used to drop the cotton ball ($t = 0.004$; $p = 0.502$, one-sided). Afterimages lasted 11.93 s on average ($SEM = 0.821$), which is in line with previous reports of ~10 s afterimages (Carlson et al., 2010; Hogendoorn et al., 2009).

3.2. Experiment 2: Training and second-order fading

An assessment of the amount of fading experienced by our participants before and after training revealed that training improved the odds of experiencing cotton ball fading by 76.36% (exp(B) = 0.567; $p = 0.037$; Fig. 2b). This is a strong indication that modifications to the representation of one's own body can be strengthened over time by extensive tool practice. Independent of training, participant's odds of experiencing fading of the cotton ball were higher (138%) when the cotton ball was dropped from the chopsticks in the dominant, as opposed to the non-dominant hand (exp(B) = 0.867; $p = 0.002$; Fig. 2b). This finding mirrors results from Experiment 1. The overall model predicted the data well (Wald Chi-Square(2) = 13.75; $p = 0.001$).

We expected improved long-term integration of the first-order tool for the trained (dominant) hand, but not for the untrained (non-dominant) hand. Hence, we also tested the impact of training on second-order object fading for both hands separately (Fig. 2b and c). Participants' odds of experiencing cotton ball fading were 215.19% increased for the dominant hand after training (exp(B) = 1.148; $p = 0.008$). This finding holds true after a strict correction for multiple comparisons ($p = 0.016$). In contrast, the non-dominant hand shows no differences before and after training (exp(B) = 0.168; $p = 0.682$).

Finally, a 2-way repeated measures ANOVA showed that the duration of the afterimage was not affected by training ($F_{(1,7)} = 1.788$; $p = 0.223$), nor the hand used to drop the cotton ball ($F_{(1,7)} = 0.853$; $p = 0.387$).

Taken together, Experiments 1 and 2 demonstrate participants' ability to integrate both first-, as well as second-order objects into the body representation, whereby the success of second-order integration changes as a function of familiarity with the first-order tool.

3.3. Skill performance and individual differences

After the 4-week training, skill with chopsticks was significantly improved ($t = 2.745$; $p = 0.029$; Fig. 3a). Interestingly, we also found a high correlation between the time spent on the skill task at baseline and skill improvement ($r = 0.921$; $p = 0.001$; Fig. 3b). This implies that participants with low baseline-skill benefited most from training. A possible explanation for this could be near-ceiling performance of high-skilled individuals at baseline. Regression toward the mean is a less likely interpretation, since participants who were slower at baseline got faster after training, whereas participants who were already fast at baseline did not really get slower. The reduction of variance after training also argues against a random redistribution of skill-test scores.

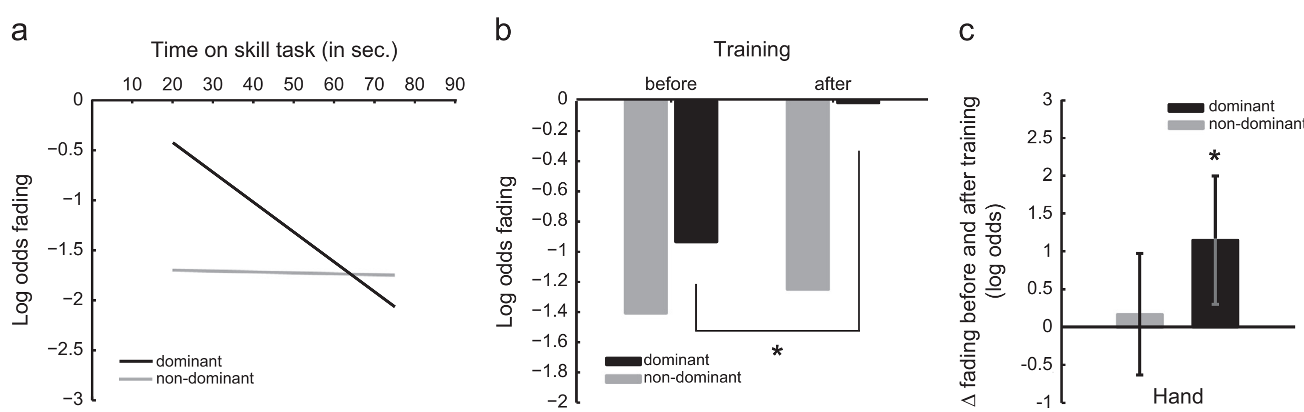

Fig. 2. Second-order object integration is modulated by skill and training. Results from the skill and training experiments, expressed in log odds of fading. Note that 50% chance of fading corresponds to log odds of zero. Log odds < 0 indicate that chances of perceiving second-order object fading were smaller than 50% (in fact, overall chances of seeing a second-order object fade were 25.8%). (a) Skill modulates fading of a distal cotton ball dropped from a pair of chopsticks. When using the dominant hand (black line, depicting fixed-effects logistic regression) participants experienced more second-order fading when they were more skilled with the first-order tool (ergo they were faster on the skill test). For highly skilled participants using their dominant hand, the log odds of seeing cotton ball fading were closer to zero, which means that they were more likely to experience fading. No such relationship between skill and fading was found when participants used their non-dominant hand (grey line). (b) Training leads to improved long-term integration of a second-order object into the body representation. After extensive chopstick practice with the dominant hand, fading experiences of the cotton ball increased to log odds of almost zero (about half of all trials) for the trained hand only (black bars). No effect of training is found for the non-dominant hand (grey bar). Bars depict the (fixed-effects) logistic regression estimates of fading before and after training, with the interaction term included. (c) Each bar depicts the difference between the log odds of fading before and after training, for each hand separately. This plot also shows that training increases the log odds of fading for the trained dominant hand, but not for the untrained non-dominant hand. Error bars indicate the 95% confidence interval around the difference scores.

Large inter-individual differences are characteristic of the way changes in positive afterimages are perceived (Davies, 1973a, 1973b). Here we find that, despite large between-subject variability (0–90% fading experienced across participants), the amount of second-order object fading within individual participants is fairly stable. The frequency of fading experiences was correlated between the dominant and non-dominant hand ($r=0.494$; $p=0.0003$). Moreover, comparing the amount of fading before and after training explains 33.87% of variance ($r=0.582$; $p=0.018$), indicating stability over time. Thus, the amount of fading a person experienced could be partly explained by individual proneness to such fading.

4. Discussion

This study demonstrates that the representation of the body can be extended beyond first-order limitations to also include second-order objects held by a tool. Participants dropped cotton balls from a pair of chopsticks, and these cotton balls faded from a stable visual scene on approximately one-fourth of all occasions. This expands the domain in which second-order fading has been demonstrated, since fading of "objects held by held objects" has not been observed before in situations where tool-use mainly relies on somatosensory and kinesthetic information from more distal parts of the hand.

We furthermore demonstrated that this fading effect was modulated by both skill and learning. Skillfulness with the first-order chopsticks actively influenced the amount of rapid integration found for the second-order cotton balls, as indexed by a higher degree of fading of these cotton balls in more-skilled participants. A slower buildup of integration was found after extensive training with the chopsticks, indicating an additional long-term component. Thus, skill and learning can interact with the extended representation of the body. No systematic changes in afterimage durations were uncovered across the various experimental conditions. This helps rule out observer bias, since we relied on subjective reports to determine both fading of imaged objects, as well as fading of the entire imaged scene. Since scene complexity was constant across conditions, the lack of variability in afterimage duration is in line with previous findings (Davies, 1973a).

After a month of practice, fading of cotton balls dropped from chopsticks in the trained (dominant) hand increased to 50% of observations. Fading of cotton balls from chopsticks in the untrained (non-dominant) hand remained unchanged, revealing the specificity of this training-induced modification of the body representation in our participants. Throughout the experiment, participants experienced more fading when using their more-skilled dominant hand (29.1–32.9%), compared to their non-dominant hand (22.4–26.3%). This difference might be explained by a general difference in lifetime-built motor fluency between the two hands; the dominant hand typically being the more practiced. Motor fluency reflects motor ability in a more general sense, and can be considered independent from tool-specific skill, which is the type of skill people acquire through (extensive) experience with a specific tool. Our results show that at very low levels of skill, similar amounts of second-order fading were experienced irrespective of the hand used. General differences in motor fluency cannot fully account for this, indicating that tool specific experiences (like those acquired during training) might prove integral for assimilation of external objects into an extended representation of the body.

Furthermore, the finding from Experiment 2 that training leads to more second-order object fading is an important one, since it allows us to draw an even more definitive distinction between general motor fluency and tool-specific skill. General motor fluency and tool-specific skill are probably often correlated, but there can be deviations between the two. To take an extreme example, a generally dexterous undergraduate student with no experience handling chopsticks might do better on the skill task from our experiment compared to a clumsy 90-year old subject who has eaten with chopsticks their whole life. Which person would see more fading? As this example demonstrates, general skill or dexterity might not necessarily mean that a person has more tool-specific experience. Thus, our first experiment does not provide an unequivocal answer to the question why people who do better on the skill test see more fading. Based on the results from Experiment 1, participants who saw more fading may have had more tool-specific skill with chopsticks, but it is also possible that these participants were simply less clumsy and more dexterous in general. The second experiment resolves this question, favoring an interpretation that stresses actual tool experience as a modulator of the fading effect.

Selective fading of an object from the afterimage has previously been considered evidence for integration of that object into the *body schema*, based on the underlying assumption that only items which are part of the body schema will fade (Carlson et al., 2010). However, any region in the afterimage where conflict arises between vision and proprioception is susceptible to fading, and fading can be

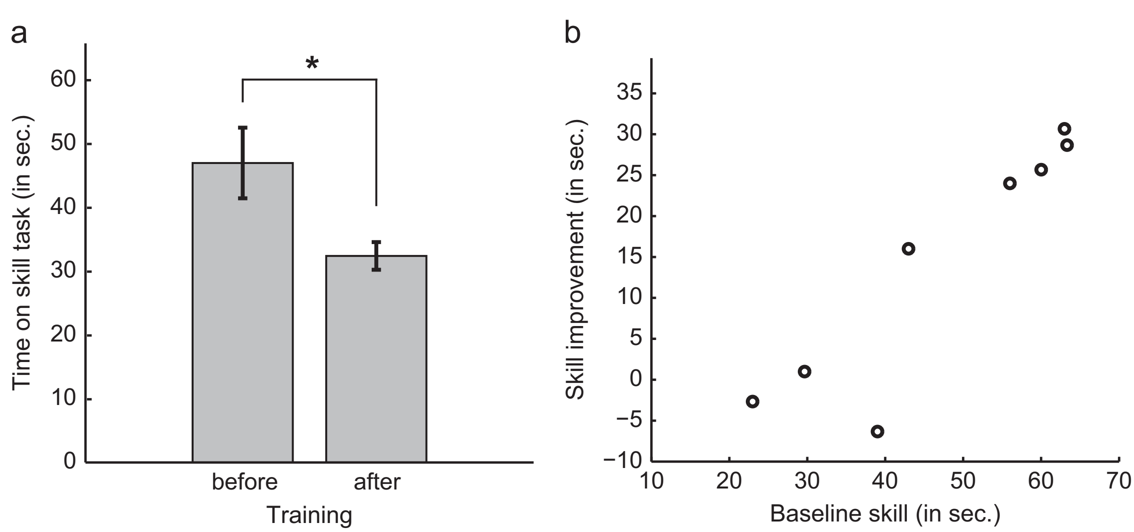

Fig. 3. Performance on chopstick-skill test, before and after training. (a) Participants needed considerably less time to perform an average skill trial after prolonged training with chopsticks ($p=0.029$). (b) Participants who were worse (slower) on the chopstick-skill test before training, appear to show the largest benefit of extensive tool practice after training. Skill improvement is defined as ($skill_{before} - skill_{after}$) in seconds.

modulated by higher-order experiences such as sense of ownership (Hogendoorn et al., 2009). Fading might therefore be more conservatively characterized as the resolution to a conflict between the visual afterimage and the expectation that forms on the basis of somatosensory and proprioceptive information—instead of proof that an object was integrated into the body schema. Thus, fading is a demonstration that we have a rich, context sensitive ability to formulate cross-modal expectations about the behavior of external objects with which we interact.

The importance of training for improved tool-integration, as indexed by fading of second-order objects from the positive afterimage, could stem from a honing of a participant's ability to differentiate amongst subtle yet complex mechanical forces sensed through dynamic touch. If such sources of information are not clearly discernable prior to training, an increased sensitivity of the haptic perceptual system could be an important requirement for becoming a more fluent tool-user. We demonstrate here that with experience, a tool that was not originally part of the body becomes capable of providing sufficiently rich cross-modal expectations about the effects of tool actions, such that the tool essentially becomes incorporated in the body representation as an effector. By incorporating a tool (chopsticks), the consequences of motor actions with that tool (releasing a cotton ball) become better predictable. Thus, the ability to flexibly map movements and their consequences proves paramount to the integration of first- and higher-order objects into the body representation.

We have assumed here that this improved link between multimodal predictions and action consequences means that tool-use modifies our representation of peripersonal space. However, what can these results tell us about the body schema, or even the body image? Probing the *body schema* can be done via tasks involving proper tool-use, which has been defined as using a tool in a way that includes a causal interaction, and contact with, the object acted upon (Cardinali et al., 2012). According to this definition, observers in our experiment were involved in actions (namely dropping a cotton ball from a pair of chopsticks) that tap into the unconscious body schema representation. Nevertheless, our observer's task was perceptual in nature, namely judging which of two cotton balls is more visible in an afterimage and giving a verbal response. Such a task does not directly explore kinematics; potential integration of the chopsticks and cotton ball into the body schema of our participants therefore remains only tentative.

Though perceptual in nature, our task also does not directly probe the way chopsticks and cotton ball are sensed by our participants, as would be required when investigating the *body image*. Instead, our study uses participant's perceptual reports as an indirect measure for an underlying system for action and tool-use. This interpretation (that our task does not probe the body image) is in line with previous research demonstrating that tools cannot be integrated into the body image (Cardinali et al., 2011, 2012). For example, grasping movements only affected the report of arm length when reports were made via a pointing movement towards a tactile stimulus on the arm (emphasizing the body schema), but not when reports and location on the arm were indicated verbally (emphasizing the body image) (Cardinali et al., 2011).

Humans have uniquely adapted for the use of tools with a flexibility and versatility that far surpasses other primates (Davies, 1973a; Seed & Byrne, 2010). Non-human primates on the other hand demonstrate relatively rudimentary tool-usage with moderate levels of inferential causal reasoning (Fujita, Kuroshima, & Asai, 2003; Goodall, 1986; McGrew, 2010; Vaesen, 2012; Visalberghi et al., 2009). Given these differences at the behavioral level, one could hypothesize that humans have evolved to naturally and rapidly assimilate first-order representations—thus having an innate capacity for tool-use (Maravita & Iriki, 2004; Peeters et al., 2009; Vaesen, 2012). Conversely, non-human primates may require substantive tool training to initiate the appropriate brain changes, which could include reorganization of somatosensory and visual signals (Ishibashi et al., 2002a; Ueno & Fujita, 1998) and the creation of novel neural connections (Hihara et al., 2006; Ishibashi et al., 2002b).

We have demonstrated here that humans can integrate not only first-, but also second-order representations, whereby the success of second-order integration changes as a function of familiarity with the first-order tool. Thus, when it comes to strengthening the feedback loop between tool perception and action consequences via training (thereby improving predictions for second-order extensions), the human situation might be akin to that of non-human primates—training is required to get the brain wired up for the task. For the time being, these conclusions remain tentative, since the task differences between most human and monkey work are substantial, and different processes could be involved.

The work presented here aims to bridge two diverging directions in the current literature, one involving rapid integration suggested by human psychophysical experiments (Bruggeman et al., 2013; Cardinali et al., 2009; Carlson et al., 2010), while the other is the much slower buildup of representations described in monkey physiology (Iriki et al., 1996). Based on the novel findings presented here, we suggest that the ability to modify body representations to include external objects can happen continuously, without previously suggested discrete limitations in terms of time and space (Carlson et al., 2010). We suggest that integration might happen anywhere along a temporal continuum: One might expect very rapid integration for highly familiar or intuitive extensions, but more limited – practice dependent – integration when items are unfamiliar. Additionally, such variations in integration speed are likely related to the amount of sensorimotor feedback provided by a tool, which can be improved via training. Also, we propose that the degree with which one can extend oneself into the environment is not constrained in an absolute sense: as the number of extensions increases, the probability of integration might drop, but such constraints could hypothetically be lifted given enough training. A more continuous view might similarly explain differences between species, with more dexterous tool-users hypothetically having more potential in terms of the possible number of extensions, or speed of integration. Future research could establish the exact limits of the capacity to incorporate objects not originally part of the body.

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