



# Testing the perceptual equivalence hypothesis in mental rotation of 3D stimuli with visual and tactile input

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## Abstract

Previous studies on mental rotation (i.e., the ability to imagine objects undergoing rotation; MR) have mainly focused on visual input, with comparatively less information about tactile input. In this study, we examined whether the processes subtending MR of 3D stimuli with both input modalities are perceptually equivalent (i.e., when learning within-modalities is equal to transfers-of-learning between modalities). We compared participants' performances in two consecutive task sessions either in no-switch conditions (Visual→Visual or Tactile→Tactile) or in switch conditions (Visual→Tactile or Tactile→Visual). Across both task sessions, we observed MR response differences with visual and tactile inputs, as well as difficult transfer-of-learning. In no-switch conditions, participants showed significant improvements on all dependent measures. In switch conditions, however, we only observed significant improvements in response speeds with tactile input (RTs, intercepts, slopes: Visual→Tactile) and close to significant improvement in response accuracy with visual input (Tactile→Visual). Model fit analyses (of the rotation angle effect on RTs) also suggested different specification in learning with tactile and visual input. In “[Session 1](#)”, the RTs fitted similarly well to the rotation angles, for both types of perceptual responses. However, in “[Session 2](#)”, trend lines in the fitting analyses changed in a stark way, in the switch and tactile no-switch conditions. These results suggest that MR with 3D objects is not necessarily a perceptually equivalent process. Specialization (and priming) in the exploration strategies (i.e., speed-accuracy trade-offs) might, however, be the main factor at play in these results—and not MR differences in and of themselves.

**Keywords** Mental rotation · Vision · Touch · Learning · Transfer-of-learning

## Introduction

The processing of visual spatial information (i.e., object features or geons, see Biederman 1987; Treisman and Gormican 1988), the synthesis of visual features into mental representations (Barquero and Logie 1999; Logie and Helstrup 1999), and the manipulation of these mental representations has interested psychologists for a long time. One special class of representation manipulation is known as mental rotation (MR; Shepard and Metzler 1971) which refers to the process of rotating a mental representation of a perceived stimulus along a mentally represented axis (e.g., imagine the letter “a” rotating to an upside down position). Although we know much about the processing of MR with visual input, we have comparatively less knowledge of the processing involved when stimuli are touched.

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## MR with visual input

One method to investigate MR is to ask participants to indicate as fast as possible whether drawings of 3D objects, presented side-by-side in varying angular orientations (i.e., 0°, 30°, 60°, etc.), are the same or different (mirror-reversed, see Shepard and Metzler 1971). The typical behavioral signature of MR is that in trials where the participants report no difference between objects (parity-trials), both response times (RT) and error rates increase with increasing rotation angle between the two depictions, while this is not the case for non-parity-trials. The linear relation of RT to rotation angle on parity-trials suggests a mental analogue to a physical rotation: the more you rotate, the longer it takes (Corballis and McMaster 1996; Kosslyn et al. 1998). These basic response patterns have been observed, for example, with alpha-numerical characters (e.g., Shepard and Cooper 1982; Dalecki et al. 2012), unfamiliar 2D shapes (e.g., polygons: Cooper 1975) and unfamiliar 3D shapes (e.g., polyhedral: Kawamichi et al. 2007; Shepard and Metzler 1971).

Neuroimaging studies commonly suggest that the “rotation” process is visual, because brain activations during MR are mainly located in specific associative visual areas in the parietal and occipital cortices (Roland and Gulyas 1994; Zhang et al. 2004; see also reviews by; Farah 1988; Finke and Shepard 1986; Kosslyn et al. 2006; Tippet 1992). However, visual experience does not preclude, in and of itself, the use of other non-visual or more general cognitive strategies. What one “visualizes” need not be a proper visual image of an object, but might only contain its spatial coordinates (see Farah et al. 1988; Kozhevnikov et al. 2005) and orientation-dependent spatial (non-visual) information (see Liesefeld and Zimmer 2013). Although the hypothesized visual nature of MR has been investigated extensively, it clearly remains a source of debate (see Kosslyn et al. 2006; Pylyshyn 2003, 1979).

## MR with tactile input

Other behavioral studies have shown that MR does not necessarily depend on visual encoding, but can be performed just as well with tactile input<sup>1</sup> (Carpenter and Eisenberg 1978; Dellantonio and Spagnolo 1990; Prather and Sathian 2002; Rösler et al. 1993; Toussaint et al. 2012). That is, active touch with movements renders accurate spatial information about an object’s location, distance, direction, and shape (Garbin 1990; Millar 2006; Lackner and DiZio 2005;

Revesz 1950) using one or both hands. Tactile representations might be constructed differently, as the time needed to optimally integrate tactile information is much longer. However, tactile response patterns have been shown to reflect similar rotation angle effects compared to the traditionally observed MR response patterns with visual input (i.e., longer RTs at higher rotation angles; Dellantonio and Spagnolo 1990; Prather and Sathian 2002). Studies also report similar activation in visual cortical areas during MR with visual and tactile inputs (Cohen et al. 1996; Wraga et al. 2005; Prather et al. 2004). Moreover, the parietal cortex is a convergent node for both visual and tactile information about the relative shape of objects (Amedi et al. 2001) and a functional area for both MR of objects with visual and tactile inputs (Cohen et al. 1996; Röder et al. 1997; Rösler et al. 1993; Tagaris et al. 1998).

Visual and tactile response similarities in MR tasks could relate to at least three accounts. (1) First, a visual dependency account states that whereas basic information uptake differs between both sensory systems, tactile information is also translated into a visual format for further perceptual and cognitive processing (Millar and Al-Attar 2002; Pascual-Leone and Hamilton 2001). (2) Second, that both sensory systems share common representations does not necessarily mean that these representations are visual. Information reaching parietal areas, following both visual and tactile information uptake, has already undergone extensive processing. The dorsal stream (to which the parietal areas belong) is considered to transmit spatial information. Thus, it is more likely that the common representations are spatial in nature and sufficiently detached from the sensory modalities through which they are derived (in contrast to sensory dependent [visual or tactile], see Liesefeld and Zimmer 2013). (3) Third, since the quality of information uptake differs between touching and seeing (Reales and Ballesteros 1999), the sensory experiences and representations of the sentient individual could also differ. For example, as touching relies extensively on the motor component of the hand and effectors, touch information is also translated from specific reference frames (i.e., the body midline axis, see Volcic et al. 2009, 2010). Under such a description, both input modalities could produce sensory-specific representations during shape perception (i.e., see Garbin 1990, 1988; Garbin and Bernstein 1984) and MR.

## Perceptual equivalence testing and learning in MR

In the present study, our aim was to test the perceptual equivalence hypothesis for MR, with natural tactile and visual 3D stimuli, using a transfer-of-learning paradigm. Under this approach, participants perform similar tasks in two consecutive sessions, each using—for the present purposes—two different perceptual modalities (Ballesteros et al. 1999; Easton

<sup>1</sup> It should be kept in mind that what is actually manipulated is the input condition, that is, either visual or tactile. Whether the actual process of MR is specific to vision and touch or more generalized is addressed with this research.

et al. 1997; James et al. 2006). The first session serves as familiarization and baseline, and the second session examines the effects of this previous experience. Significant learning transfer (i.e., percent improvements in “[Session 2](#)”, compared to baseline results in “[Session 1](#)”) suggests similar processing and that information can be shared between both perceptual modalities. When both transfer-of-learning directions (visual→tactile and tactile→visual) show identical improvements to both within-modality learning situations (visual→visual and tactile→tactile), this meets the requirement for perceptual equivalence (Garbin 1988; Hatwell 2000; Streri 2000).

Our participants were divided into four groups, and completed two consecutive MR tasks either in the same perceptual modalities (no-switch conditions: Visual→Visual [V→V] and Tactile→Tactile [T→T]) or in different perceptual modalities (switch conditions: Visual→Tactile [V→T] and Tactile→Visual [T→V]). Whether each condition showed similar learning in “[Session 2](#)” tasks in comparison to baseline “[Session 1](#)” tasks was the critical question to test the perceptual equivalence hypothesis for MR. Asymmetries in improvements between switch (and no-switch) conditions could also warrant the consideration of differences in processing (Hatwell 2000), and therefore, a certain dependency on sensory specific experience.

Similar to the present study, Toussaint et al. (2012) had their participants perform the Mental Rotation Test (MRT, Vandenberg and Kuse 1978) in two consecutive sessions, either under switch or no-switch conditions. This was done to determine whether MR abilities overlap or are more specific to a given sensory modality. For switch conditions, they only observed transfer-of-learning for accuracy, but not for RTs—which could suggest sensory specific influences on visual and tactile MRT performances. Since the MRT is not a pure measure of MR (see Caissie et al. 2009), Toussaint et al. (2012) treated their results with caution. The critical difference in the present study is that we used an experimental approach with a manipulation of rotational angle in an MR task, instead of (versions of) a psychometric test. We also used two additional response parameters—the intercept and the slope of the model relating response times to rotation angle—to investigate learning in MR (see Provost et al. 2013).

The intercept reflects the baseline of perceptual encoding and confirmation processes (e.g., basic encoding of object shapes, object comparisons, response selection, Shepard and Metzler 1988) as well as recoding of stimuli into MR-compatible representations (see Liesefeld and Zimmer 2013). The slope reflects the speed of MR (Bethell-Fox and Shepard 1988; Cohen and Blair 1998; Dror and Kosslyn 1994). However, these two parameters are not mutually exclusive in the context of MR, and we used this distinction only as one of many possible indications (with caution). The slope

very likely reflects only processes specific for MR, but some MR-specific processes likely contribute also to the intercept. In our transfer design, improvements in MR performances from “[Session 1](#)” would be reflected by decreasing slope and intercept values in “[Session 2](#)”.

Learning effects, specifically for MR, have received much attention, but their underlying mechanisms remain poorly understood. For some researchers, learning in MR is dependent on context repetition, and does not necessarily generalize to new (perceptual) contexts (Heil et al. 1998; Provost et al. 2013; Tarr and Pinker 1989). Heil and colleagues (1998) have suggested that learning is dependent on the repetition of object perspective views, occurring only in test conditions very similar to the familiarization conditions. For other researchers, training changes the nature of the cognitive sub-routines (i.e., speed of MR) and the repetition of similar processes should speed up performances (see Wallace and Hofelich 1992; Bethell-Fox and Shepard 1988). That is, learning is independent of the particular type of perceptual input (Stigler et al. 1988), as long as the same internal processes are involved. In particular, transfer-of-learning will strongly depend on the similarity of participants’ stored visual and tactile representations—and processing of these representations—during MR.

## Performance measures in MR and predictions

For the present purposes, we considered analyses on two performance measures: accuracy and RT; and made inferences on the slope and intercept parameters of the thus derived RT functions. Whether performance patterns with both visual and tactile input complied similarly with traditionally observed MR patterns was assessed at baseline (“[Session 1](#)”). We evaluated transfers-of-learning (switch condition) and learning (no-switch condition) from “[Sessions 1](#)” to “[Session 2](#)”, on slope and intercept parameters. We further conducted contrast analyses—using fit statistics—to relate the effects of rotation angle to MR in both perceptual modalities. Three sets of predictions can be formulated. (1) We expected that both visual and touch responses match the traditionally observed MR response signatures (Shepard and Metzler 1971; Prather and Sathian 2002). (2) We expected improvements, that is, positive transfer, in the no-switch conditions from “[Sessions 1](#)” to “[Session 2](#)” (Heil et al. 1998; Provost et al. 2013). The critical question, however, was whether the improvement would be the same also for the switch conditions. Observing differences between switch conditions and no-switch conditions would suggest that MR can solicit sensory specific processes/representations (Garbin 1990; Hatwell 1983, 2000; Streri 2000). However, if the MR strategy is perceptually equivalent, we expected no differences between conditions. (3) Finally, we expected a linear fit of RTs to rotation angle,

which would unequivocally relate effects of rotation angle to MR in both perceptual conditions, at both “[Sessions 1](#)” and “[Session 2](#)”.

## Methods

### Participants

Fifty-six right-handed adults (mean age 21.78 years, 26 females) from the Poitiers area in France voluntarily participated in this study. They reported normal or corrected-to-normal vision and no tactile sensory loss. All participants were treated according to the guidelines given by the WMA Declaration of Helsinki for research involving human subjects (World Medical Association 2013, para. 26).

### MR tasks and experimental setup

Both MR tasks, with tactile and visual input, consisted each of a presentation of 56 pairs of 3D cubes modelled after the Shepard and Metzler (1971) stimuli. Each pair presented a model to the left and a comparison object to the right (per task: 28 parity and 28 non-parity pairs). Participants were to indicate as fast as possible whether the two objects were the same or different. We created four model objects for our purposes (see Fig. 1a). Each object consisted of an assembly of ten wooden cubes, forming a 3D object with four segments and three right angles. The objects were placed on steel fixations (length ~3.5 cm; diameter = 0.3 cm) and centered on wooden presentation boards (eight boards 40 cm × 20 cm), 15 cm apart (see Fig. 1b). For each presentation board, the comparison objects could be rotated to seven different positions relative to the model objects, varying in rotation angles up to 180° (0°; 30°; 60°; 90°; 120°; 150°; 180° on the z-axis). The comparison objects were either the same or—in the case of non-parity-trials—mirrored versions of the model objects. Fifty-six pairs were presented per session in both the tactile and visual tasks: 4 models × 2 response possibilities (parity and non-parity) × 7 rotation angles.

Participants were seated facing an experimental box. Each trial board was positioned 60 cm at a downward angle of 35° from the participants’ eyes. The trial boards were positioned 40 cm above the surface of the working table (within reach of participants’ right hand in the tactile modality). Exploration for every trial started on the model (on the left). In both perceptual modalities, participants gave parity judgments with the middle and index fingers of their left hand, using response keys (parity or non-parity). Figure 1c

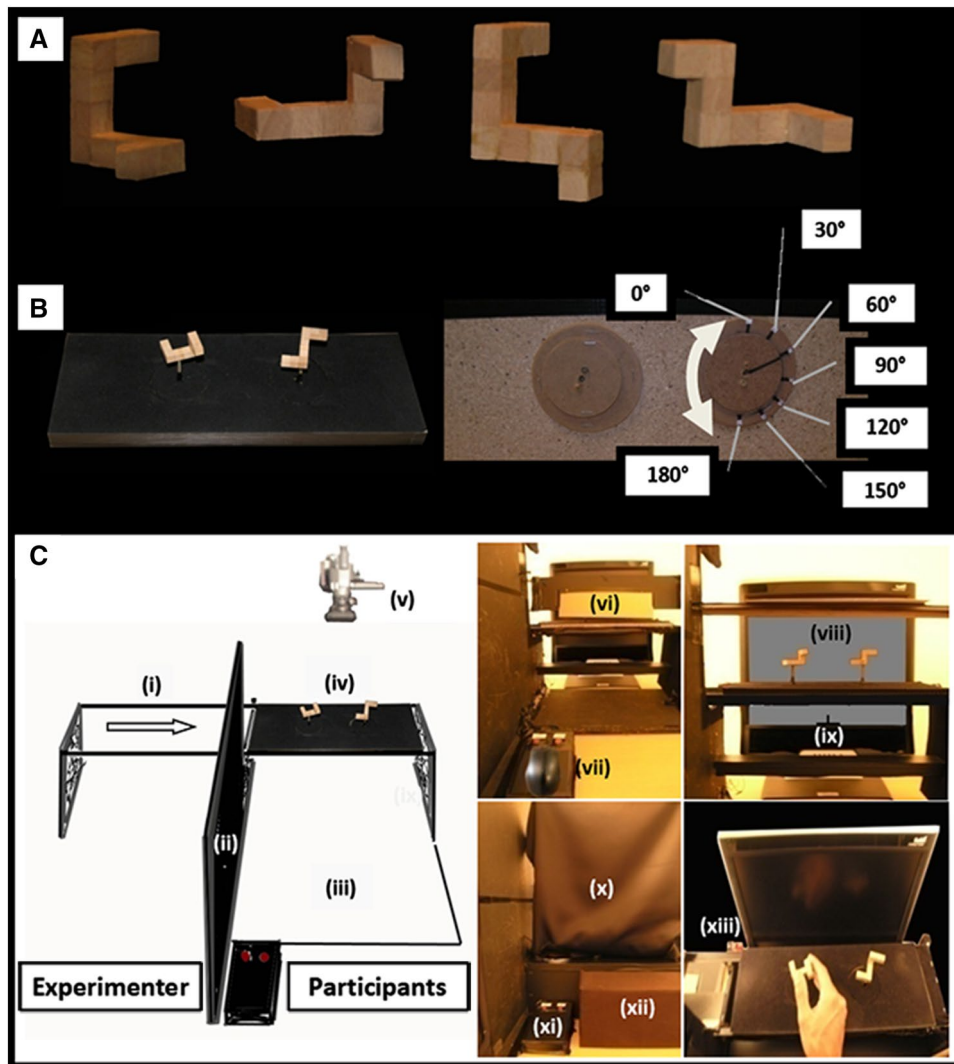
illustrates the experimental box and response modalities for both perceptual tasks.

### Groups and procedure

Participants were randomly assigned to one of four groups. They either performed two successive “[Sessions 1](#)” and “[Session 2](#)” in the same perceptual modalities (No-switch: T→T and V→V) or in different perceptual modalities (Switch: V→T and T→V). Overall, 112 object pairs were administered to each participant. The 56 pairs in “[Session 1](#)” were repeated during “[Session 2](#)”, and administered within each session in a random order. For each session, participants received the same instructions. Four practice trials were used to familiarize participants with the particular equipment, and the experimenter made sure the instructions were understood (note: the practice trials were not repeated during the experiment). No performance feedback was given during the actual experiment. Participants were given a 5-min break between task sessions, i.e., the time needed by the experimenter to calibrate and prepare the equipment for the next session. The experiment lasted approximately 1 h.

### Visual task: response recording and RT definitions

RT measurement in the visual modality was based on eye-movement recording, using the non-intrusive ©Tobii 120X eye-tracking system which consists of a 17-in. screen connected to a computer. The screen was placed behind the object pairs in a way to avoid interference and loss of signal with the system cameras and infrared pupil markers (the height of the object presentation rails was at ¼ from the base of the screen). The objects were centered vertically and horizontally in front (10 cm) of the screen. Optimal measurement also required adequate lighting on the objects. A basic grey scale (R:G:B = 128:128:128) on-screen minimized screen brightness and eliminated image persistence after-effects during trials. A chin rest was used to avoid loss of threshold from unnecessary head movements (viewing distance of approximately 60–70 cm). Eye movements were recorded with a sampling rate of 60 Hz and a constant precision of 0.5°. Several pre-tests ensured that measurement was optimal throughout the data collection (i.e., from first fixation on-trial to response selection). Prior to starting the visual task, the eyetracker was calibrated using a standard coordinate fixation procedure. Between trials, participants fixated a visual cross at the bottom of the screen, which guaranteed ongoing calibration and measurement during the visual task. The program recorded participants’ responses, and RTs were defined as starting with the first ocular fixation on the displayed



**Fig. 1** **a** Four models used for the construction of parity and non-parity-trials. **b** Left: example of a parity-trial with the model to the left and the comparison object to the right (15 cm apart). Right: view from underneath the boards, with the rotation system for the comparison object at seven possible rotation angles (0°; 30°; 60°; 90°; 120°; 150°; 180°). **c** Illustration of the experimental box and work space for both perceptual modalities. (i) Rail system used to slide object pairs in position for each trial. (ii) Opaque screen between experimenter and participants. (iii) Work space. (iv) Position of object pairs during both perceptual modalities. (v) Video camera filmed the right

hand on the objects. (vi) Mechanical door for visual task entry on the object pairs. (vii) Response keys (computer mouse buttons for the visual task). (viii) ©Tobii 120X screen for recording eye movements. (ix) Between trials visual fixation cross. (x) Opaque visual occlusion screen used during tactile task (participants placed their right arm through an entry slot at the bottom of this screen to touch the objects). (xi) Response keys (light switches for the tactile task). (xii) Right arm rest. (xiii) Lights to signal the response and nature of response, and to alert the experimenter to switch trials during both tactile and visual tasks

objects until a response key was pressed (this was to equate with the tactile RT definition, see below).

**Tactile task: response recording and RT definitions**

For the tactile modality, participants’ performances were filmed using a digital camera. Video sequencing of tactile inspection was done using the Actogram Kronos™ software. Video sequences included the right hand touching the objects and two response activated lights (for parity

and non-parity responses, respectively). Once activated, the lights signaled participants’ response choices. Participants were instructed to use their right hand, and access to the two objects was not constrained (i.e., use of all fingers and hand in whichever angle was best suited to the individual’s input approach). RT per trial was calculated in seconds, beginning with the first inspection (i.e., when the hand first touches the model) until a response key was pressed (note: left-hand finger response switches were designed to mimic the response switches used in the visual task).

## Data treatment and analyses

Of the total 56 participants, data from one participant were excluded because he/she reached accuracy levels around 50% (chance level). Further, 43 of the total 6272 trials in the trial list encountered problems and were thus rejected/non-collected (0.7%, 20 parity-trials and 23 non-parity-trials = 18 tactile trials and 25 visual trials). Stimulus rotation angles were collapsed into four variable levels: 0° (null rotation angle), 30°–60° (low rotation angle), 90°–120° (medium rotation angle), 150°–180° (high rotation angle), to reach a sufficient number of correct trials per resulting cell (and thereby to avoid empty cells).<sup>2</sup> Both types of trials (parity vs. non-parity) were treated separately and only the main analyses on parity-trials are reported (see “Results” section).<sup>3</sup> Accuracy was calculated as the percentage of correct trials for each rotation angle level. RTs deviating more than 2.5 standard deviations from the mean (calculated separately for each participant and design cell, within rotation angle levels) were excluded as outliers (3.5%).<sup>4</sup> Corrected mean RTs were then calculated for every rotation angle level. Accuracy and RT data were given the same treatment in both “Sessions 1” and “2”. We applied a significance criterion of  $\alpha = 0.05$  for all analyses.

“Session 1” analyses examined whether differences appeared between participants’ MR performances with tactile and visual inputs. We assessed whether the visual and tactile response patterns complied similarly with traditional response patterns, which would suggest that participants perform a MR on parity-trials (Shepard and Metzler 1971). “Session 2” analyses examined the effect of previous sensory experience (i.e., switch condition vs. no-switch condition). For “Session 1”, both dependent measures were submitted to a 2 Perceptual Modality (tactile vs. visual)  $\times$  4 Rotation Angle (0°, 30°–60°, 90°–120°, and 150°–180°) ANOVA. For “Session 2”, the dependent variables were submitted to a 2 Perceptual Modality (in “Session 2”)  $\times$  2 Switch (switch condition vs. no-switch condition)  $\times$  4 Rotation Angle ANOVA. We then carried out ANOVAs with Perceptual

Modality as the single variable (“Session 1”) or with Perceptual Modality  $\times$  Switch (“Session 2”) on the slope and intercept values of the function relating RTs and Rotation Angle (see below for calculation of these measures). While Perceptual Modality and Switch were between-participants variables, we treated Rotation Angle as a repeated-measure.

Slope and intercept values were calculated as a function of the RT data on all seven rotation angles, only for correctly responded to parity-trials. To further quantify changes from “Sessions 1” to “Session 2” (i.e., performance improvement or performance decrement for slope and intercept), we computed the change in performances from “Session 1” to “Session 2” relative to a baseline measure (we refer to this as the *change rate* and express this as a percentage). As the baseline, we used “Session 1” data collapsed across participants in the no-switch condition and across participants in the switch condition ( $\text{baseline}_{\text{tactile}} = \text{average of tactile performances in “Session 1” for T} \rightarrow \text{T and T} \rightarrow \text{V groups}$ ;  $\text{baseline}_{\text{visual}} = \text{average of visual performances in “Session 1” for V} \rightarrow \text{V and V} \rightarrow \text{T groups}$ ; see Toussaint et al. 2012, for a similar procedure). Change rate was calculated as the difference between “Session 2” performance and the respective baseline (average across participants), divided by this baseline (and multiplied by 100). We report positive change rates as indicating improvements in the intercept values and slope values. Negative change rates indicate deterioration in performance (i.e., slope increase and intercept increase).<sup>5</sup> For change rates, the most interesting results concern effects of Perceptual Modality and Switch. We therefore ran a 2 Perceptual Modality (tactile vs. visual)  $\times$  2 Switch (switch condition vs. no-switch condition) ANOVA on both slope and intercept change rate dependent measures.

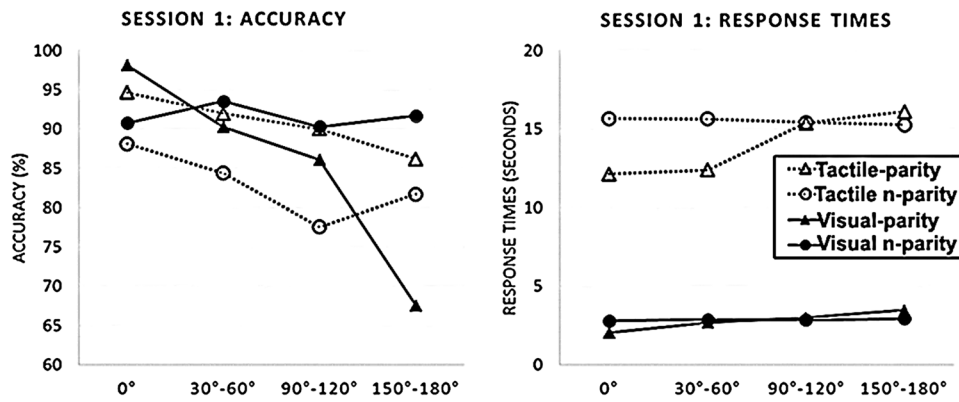
We further conducted contrast analyses to relate the effects of Rotation Angle to MR for both tactile and visual responses. Two curves (a line and a parabola) were fit for each Perceptual Modality (tactile vs. visual) for “Session 1” and as a function of Switch (switch vs. no-switch) for “Session 2”. Participants’ responses were analyzed within-modalities in “Session 1”. In the second Session, each group subtype (T–T, V–V, V–T, T–V) was treated separately. Fitting was achieved via MATLAB 2016b (MathWorks)’s “curve fitting toolbox”. Because of the presence of significant outliers in the cleaned data across rotation angles, the

<sup>2</sup> It would have been preferable to administer more trials per participant. However, tactile sessions conceivably required longer responses per trial and thus more experimentation time, rendering it impractical to administer more trials for each rotation angle cell per participant. As a result, the reader should keep in mind that between-subjects effects could have low power and that the estimates of mean RTs and accuracies are not as reliable, compared to traditional MR studies.

<sup>3</sup> We invite the interested reader to consult non-parity response analyses in the “Appendix A2”. Since it is less clear which processes sub-tend solving these trials, our main analyses focused on parity-trials which specifically require MR processing (i.e., objects are the same).

<sup>4</sup> For trial-wise outlier rejection, different methods were trialed giving similar results (e.g., log transformed RTs, interquartile range cut-off).

<sup>5</sup> Therefore change rates for slopes and intercepts were calculated as  $\text{CR} = [(\text{baseline} - \text{“Session 2”}) / \text{baseline}] \times 100$ . Both switch and no-switch group performances in “Session 2” were compared to the same averaged baseline in “Session 1”. In the case of no-switch groups, no significant difference was rendered between actual performances and the average baseline calculation. This average calculation ensured a comparison of switch group performances for the participants that did not actually repeat the same set of trials in both “Session 1” and “Session 2”.



**Fig. 2** Left: “Session 1” mean accuracy as a function of Perceptual Modality (tactile vs. visual) and Parity type (Parity vs. Non-parity) at every Rotation Angle (0°, 30°–60°, 90°–120°, 150°–180°). Right: “Session 1” mean correct RTs as a function of Perceptual Modality

and Parity type at every Rotation Angle. Note: average accuracy for non-parity-trials is only featured here for direct comparison with parity responses, although we did not feature them in the main analyses

fit was weighted using the standard deviation of the observations across each rotation angle, and was made robust using a least absolute residuals (LAR) algorithm. The LAR method minimizes the absolute difference in the residuals rather than the squared differences. This allows the extreme values to have a lesser influence on the minimization procedure.

## Results

### Session 1

Mean accuracy is visualized in Fig. 2 (left panel) and summarized in Table 1 (see “Appendix” section). The ANOVA revealed a main effect of Perceptual Modality,  $F(1,53) = 4.20, p = 0.045, \eta_p^2 = 0.07$ , a main effect of Rotation Angle,  $F(3,159) = 24.72, p < 0.001, \eta_p^2 = 0.32$ , as well as an interaction between these variables,  $F(3,159) = 8.31, p < 0.001, \eta_p^2 = 0.14$ . Participants made fewer errors on tactile compared to visual trials ( $90.7 \pm 8.3$  vs.  $82.9 \pm 15.3\%$ ), with this distinction being more important at higher rotation angles. Figure 2 (left panel) also suggests a greater effect of Rotation Angle on participants’ responses in the visual modality. Thus, we further analyzed the Accuracy data, within both perceptual modalities separately, via ANOVAs with Rotation Angle as a single factor. Whereas participants’ responses in the tactile modality were not affected significantly by the level of Rotation Angle,  $F(3,81) = 3.25, p = 0.042, \eta_p^2 = 0.11$ , participants’ responses in the visual modality showed a strong main effect of Rotation Angle,  $F(3,78) = 24.16, p < 0.001, \eta_p^2 = 0.48$ .

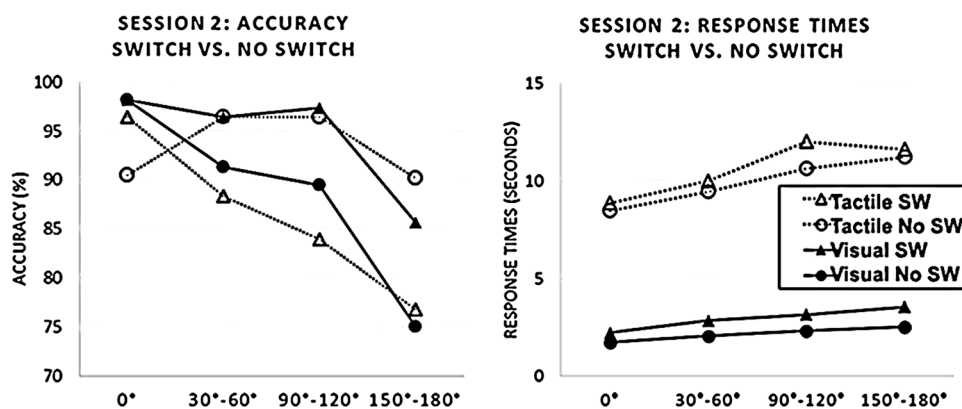
Mean correct RTs are visualized in Fig. 2 (right panel) and are summarized in Table 1 (see “Appendix”).<sup>6</sup> The ANOVA revealed main effects of Perceptual Modality,  $F(1,53) = 78.76, p < .001, \eta_p^2 = 0.60$ , Rotation Angle,  $F(3,159) = 29.91, p < .001, \eta_p^2 = 0.36$ , as well as an interaction between these variables,  $F(1,159) = 10.27, p < .001, \eta_p^2 = 0.16$ . As expected, participants’ responses in the tactile condition generally required more time than participants’ responses in the visual condition ( $14.0 \pm 6.5$  vs.  $2.8 \pm 0.9$  s). Figure 2 (right panel) also suggests different effects of the Rotation Angle, depending on the perceptual modality. Thus, we further analyzed RT data, within both perceptual modalities, via ANOVAs with Rotation Angle as a single factor. Participants’ responses seemed not to be affected differently by the level of Rotation Angle in both perceptual modalities, tactile:  $F(3,81) = 19.86, p < .001, \eta_p^2 = 0.42$ , and visual:  $F(3,78) = 31.57, p < .001, \eta_p^2 = 0.55$ . However, ANOVAs with Perceptual Modality as the single variable also showed that slopes,  $F(1,53) = 16.42, p < .001, \eta_p^2 = 0.24$  (visual:  $7.7 \pm 5.3$  ms/°, tactile:  $27.1 \pm 24.3$  ms/°), as well as intercepts,  $F(1,53) = 65.76, p < .001, \eta_p^2 = 0.55$  (visual:  $2.2 \pm 0.7$  s, tactile:  $11.7 \pm 6.0$  s), markedly differ between the response patterns obtained in both perceptual modalities.

### Session 2

Mean accuracy is visualized in Fig. 3 (left panel). The ANOVA on accuracy only revealed a main effect of Rotation Angle,  $F(1,51) = 12.14, p < .001, \eta_p^2 = 0.19$ , and two significant interactions: Perceptual Modality  $\times$  Switch,  $F(1,52) = 7.94, p = .007, \eta_p^2 = 0.13$ , and Perceptual

<sup>6</sup> The interested reader is also invited to consult “Session 1” and “Session 2” analyses on non-parity-trials in the “Appendix A2”.

**Fig. 3** Left: “Session 2” mean accuracy as a function of Perceptual Modality (tactile vs. visual) and Switch condition (Switch vs. No-switch) at every Rotation Angle (0°, 30°–60°, 90°–120°, 150°–180°). Right: “Session 2” mean correct RTs as a function of Perceptual Modality and Switch condition at every Rotation Angle (*sw* switch condition, *no-sw* no-switch condition)



Modality  $\times$  Switch  $\times$  Rotation Angle,  $F(3,153) = 3.74$ ,  $p = .021$ ,  $\eta_p^2 = 0.07$ . We thus further analyzed the data from both perceptual modalities separately via Switch  $\times$  Rotation Angle ANOVAs. For participants' tactile response patterns, we observed a Switch effect,  $F(1,26) = 4.30$ ,  $p = .048$ ,  $\eta_p^2 = 0.14$ , a significant Rotation Angle effect,  $F(3,78) = 3.67$ ,  $p = .007$ ,  $\eta_p^2 = 0.26$ , and a significant interaction between Switch and Rotation Angle,  $F(3,78) = 3.66$ ,  $p = .016$ ,  $\eta_p^2 = 0.12$ . Participants in the switch condition (Visual–Tactile) obtained significantly lower tactile accuracy at higher rotation angles compared to participants in the no-switch condition (Tactile–Tactile). For participants' visual response patterns, we also observed a trending (marginally above the alpha value) Switch effect of the opposite direction,  $F(1,25) = 3.67$ ,  $p = .067$ ,  $\eta_p^2 = 0.13$ , and a significant Rotation Angle effect,  $F(3,75) = 9.07$ ,  $p = .001$ ,  $\eta_p^2 = 0.27$ . Participants in the switch condition (Tactile–Visual) tended to obtain better accuracies, compared to participants in the no-switch condition (Visual–Visual). While participants' prior tactile experience tended to improve their response accuracy in the visual task (in “Session 2”), participants' prior visual experience was non-beneficial for their response accuracy in the tactile task.

Mean correct RTs for parity-trials are visualized in Fig. 3 (right panel). ANOVAs for RTs revealed main effects of Perceptual Modality,  $F(1,51) = 120.33$ ,  $p < .001$ ,  $\eta_p^2 = 0.70$  (T > V), and Rotation Angle,  $F(3,153) = 33.87$ ,  $p < .001$ ,  $\eta_p^2 = 0.40$ , and a significant interaction between both variables,  $F(3,153) = 8.65$ ,  $p < .001$ ,  $\eta_p^2 = 0.15$ . Neither a main effect nor any interactions involving Switch were significant ( $F_s \leq 1.06$ ). We further analyzed the data from both perceptual modalities separately to mirror the accuracy analysis for “Session 2”, via Switch  $\times$  Rotation Angle ANOVAs. For participants' tactile response patterns, we observed the expected Rotation Angle effect,  $F(3,78) = 20.67$ ,  $p < .001$ ,  $\eta_p^2 = 0.44$ , but no Switch effects ( $F_s < 1$ ). For participants' visual response patterns, we observed a significant Switch effect,  $F(1,25) = 8.66$ ,  $p = .007$ ,  $\eta_p^2 = 0.26$ , and the expected Rotation Angle effect,  $F(3,75) = 35.34$ ,  $p < .001$ ,  $\eta_p^2 = 0.59$ .

Participants in the switch condition (Tactile–Visual) obtained significantly longer RTs compared to participants in the no-switch condition (Visual–Visual). A tactile prior experience was thus non-beneficial for the response speeds in the visual task.

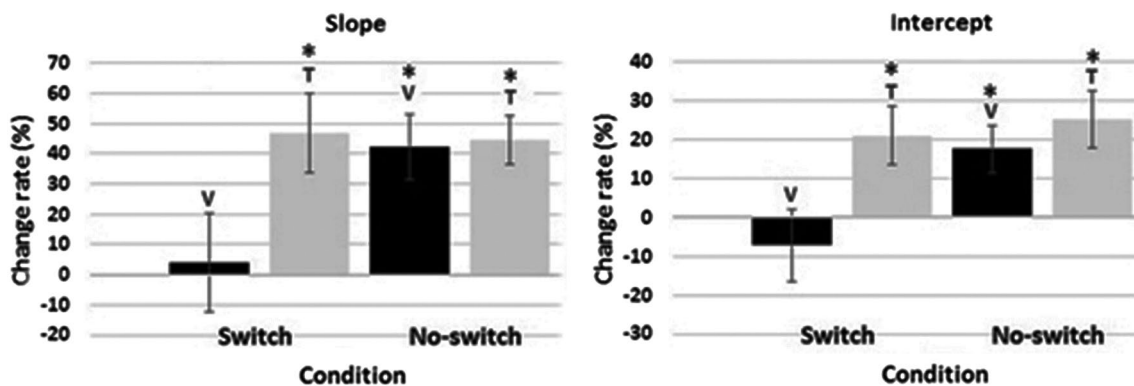
Two-way ANOVAs with Perceptual Modality and Switch as variables also showed that slopes,  $F(1,51) = 11.42$ ,  $p < .001$ ,  $\eta_p^2 = 0.19$  (visual:  $5.9 \pm 4.1$  ms/°, tactile:  $16.9 \pm 16.1$  ms/°), and intercepts,  $F(1,51) = 117.86$ ,  $p < .001$ ,  $\eta_p^2 = 0.70$  (visual:  $2.1 \pm 0.7$  s, tactile:  $9.0 \pm 3.2$  s), markedly differ between participants' visual and tactile response patterns. No switching effects, nor interactions between both variables, were observed ( $F_s \leq 1.14$ ).

### Change rate analyses

We compared participants' respective slope and intercept change rates, as a function of Perceptual Modality and Switch in “Session 2” (see Fig. 4). Further interpretations of the main analyses will refer to *t* test results that evaluate whether change rates by dependent measures and by groups significantly differ from zero. ANOVA results on *slope* change rates revealed no effect of Perceptual Modality, nor Switch, and no significant interactions between these variables (all  $F_s \leq 2.63$ ). Significant change rates were, however, observed in the no-switch conditions (V  $\rightarrow$  V,  $t(12) = 3.89$ ,  $p = .002$ ,  $d = 1.53$ , and T  $\rightarrow$  T,  $t(13) = 5.52$ ,  $p < .001$ ,  $d = 2.09$ ) and prior visual switch condition (V  $\rightarrow$  T,  $t(13) = 3.59$ ,  $p = .003$ ,  $d = 1.36$ ), as the descriptive patterns also suggest (see Fig. 4). In these conditions, prior visual experience speeds up participants' MR, whereas tactile prior experience has no effect on the speed of MR for participants in the visual modality (T  $\rightarrow$  V,  $t(13) = 0.24$ ,  $p = .814$ ,  $d = 0.09$ ).

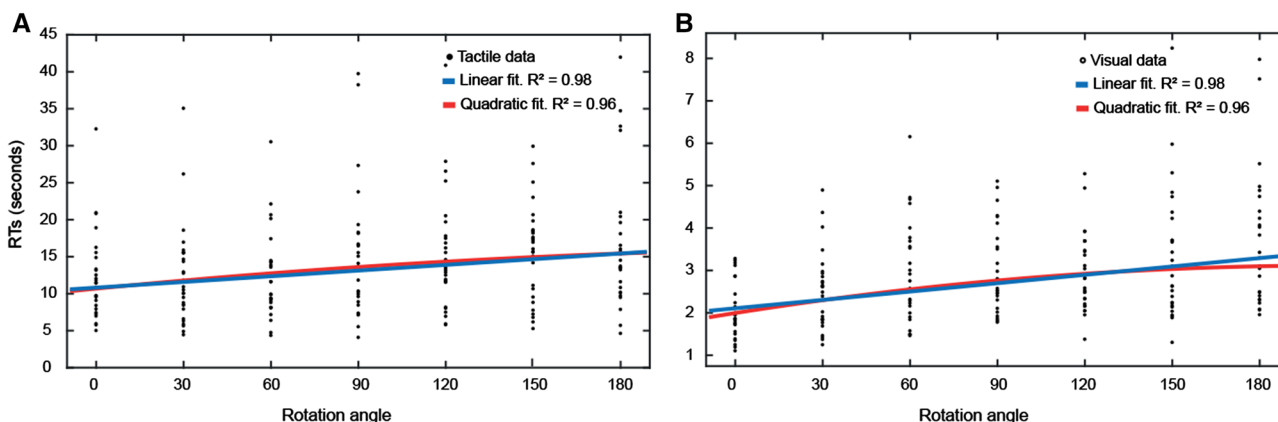
ANOVA results on *intercept* change rates revealed a significant effect of Perceptual Modality,  $F(1,51) = 5.44$ ,  $p = .024$ ,  $\eta_p^2 = 0.10$ , a close to significant effect (marginally above the alpha value) of Switch,  $F(1,51) = 3.43$ ,  $p = .070$ ,  $\eta_p^2 = 0.06$ , but no significant interaction between these variables,  $F(1,51) = 1.78$ ,  $p = .100$ ,  $\eta_p^2 = 0.05$ . In the





**Fig. 4** “Session 2” change rates on parity-trials by dependent measures (slope, intercept) as a function of Switch (switch and no-switch) and Perceptual Modality in “Session 2” (V visual and T tactile). Posi-

tive transfer: improvement; negative transfer: deterioration. Error bars represent one  $\pm$  standard error for every change rate. Asterisks mark an improvement significantly different from zero ( $p_s < 0.05$ )



**Fig. 5** Linear and quadratic fit statistics for both tactile and visual input responses on parity trials at baseline. **a** Tactile responses; **b** visual responses

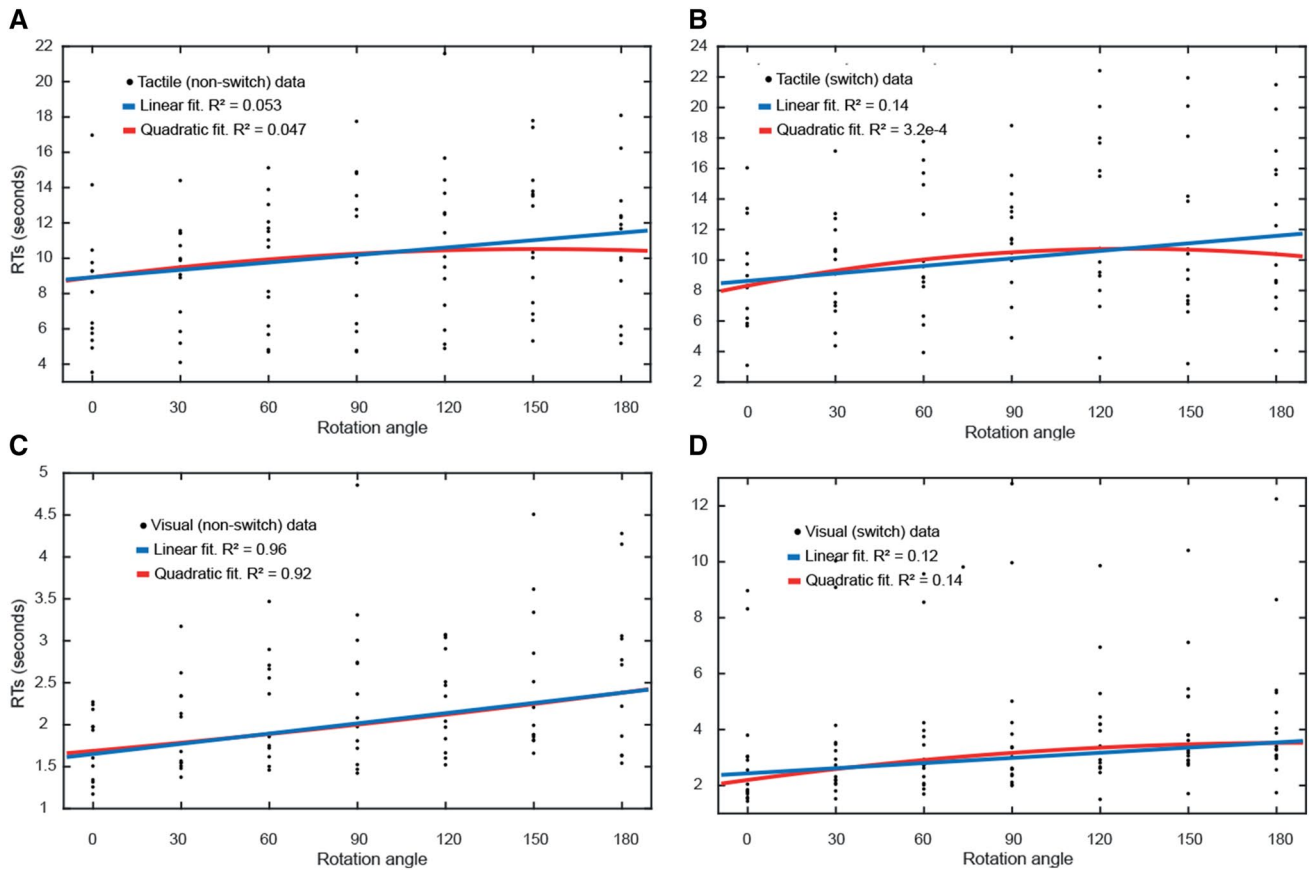
no-switch conditions and the tactile switch condition, participants’ improvement is significant (V→V,  $t(12) = 2.88$ ,  $p = .014$ ,  $d = 1.13$ , T→T,  $t(13) = 3.46$ ,  $p = .004$ ,  $d = 1.31$ , V→T,  $t(13) = 2.78$ ,  $p = .016$ ,  $d = 1.05$ ). For the visual switch condition (T→V), participants do not show improvement,  $t(13) = -0.76$ ,  $p = .461$ ,  $d = -0.29$ . This confirms that participants’ prior tactile experience is non-beneficial for their visual processing in “Session 2”, while participants’ prior visual experience speeds up their subsequent tactile processing, similar to improvements observed with participants in no-switch conditions.

### Linear and quadratic fit statistics<sup>7</sup>

In the baseline phase of the experiment, i.e., “Session 1”, the mean curve across participants regressed to a linear function (see Fig. 5). We found that both the linear and the quadratic functions fit the data equally well across tactile and visual input responses ( $R^2_{\text{visual-linear}} = 0.98$ ,  $R^2_{\text{visual-quadratic}} = 0.96$ ,  $R^2_{\text{tactile-linear}} = 0.98$ ,  $R^2_{\text{tactile-quadratic}} = 0.98$ ).

However, after being informed by one perceptual modality to the other, i.e., when the participants are asked to switch perceptual modalities (“Session 2”), stark differences were observed in the trend lines (see Fig. 6). Specifically, when participants switch from the visual to the tactile modalities, the data regresses weakly to a linear model ( $R^2_{\text{visual-linear}} = 0.14$ ,  $R^2_{\text{visual-quadratic}} = 0.00032$ ). Whereas when participants switch from the tactile to the visual modalities, the data take on a non-linear relationship to the rotation angle ( $R^2_{\text{tactile-linear}} = 0.12$ ,

<sup>7</sup> The interested reader is also invited to consult “Session 1” and “Session 2” Accuracy and RT to rotation angle correlational analyses in the “Appendix A3”.



**Fig. 6** Linear and quadratic fit statistics for subgroups in “Session 2”, with similar (no-switch: **a** T–T and **c** V–V) and different (switch: **b** V–T and **d** T–V) prior perceptual experience

**Table 1** “Session 1” descriptive statistics for Accuracy and RTs as a function of Perceptual Modality (tactile vs. visual), Parity type (parity vs. non-parity), and Rotation Angle (Means ± SD)

	Tactile		Visual	
	Accuracy %	RT secs	Accuracy %	RT secs
Parity-trials				
0°	94.64 ± 10.44	12.12 ± 5.80	98.14 ± 6.67	2.06 ± 0.65
30°–60°	91.96 ± 9.75	12.38 ± 6.16	90.27 ± 12.66	2.70 ± 0.99
90°–120°	89.90 ± 14.74	15.37 ± 8.01	86.11 ± 15.63	2.99 ± 0.90
150°–180°	86.16 ± 13.75	16.09 ± 7.05	67.59 ± 23.06	3.47 ± 1.51
N.-parity-trials				
0°	88.09 ± 16.26	15.65 ± 9.33	90.74 ± 14.12	2.79 ± 1.31
30°–60°	84.37 ± 20.01	15.63 ± 6.83	93.51 ± 11.16	2.87 ± 1.10
90°–120°	77.55 ± 19.88	15.42 ± 6.52	90.28 ± 17.10	2.86 ± 0.99
150°–180°	81.69 ± 19.68	15.26 ± 6.64	91.67 ± 10.96	2.95 ± 1.03

$R^2_{\text{tactile-quadratic}} = 0.14$ ). Within both perceptual modalities, while the linear and quadratic trends are comparable, the relationship of the reaction times to the rotation angle assumes a much larger variance in the tactile modality ( $R^2_{\text{tactile-linear}} = 0.053$ ,  $R^2_{\text{tactile-quadratic}} = 0.047$ ,  $R^2_{\text{visual-linear}} = 0.96$ ,  $R^2_{\text{visual-quadratic}} = 0.92$ ).

### Discussion

In the present study, we tested whether MR of 3D stimuli is a perceptually equivalent process by directly comparing participants’ performances in two consecutive task sessions, with either visual input or tactile input. Two groups

of participants performed twice in the same perceptual modality (no-switch conditions:  $V \rightarrow V$  and  $T \rightarrow T$ ), and two other groups performed one session with visual stimuli and the other session with tactile stimuli (switch conditions:  $V \rightarrow T$  and  $T \rightarrow V$ ). Here, we first discuss three sets of predictions as outlined in the “[Introduction](#)” section. The first pertains to the traditionally observed MR responses (i.e., that response patterns should comply with traditionally observed MR signatures independent of the perceptual inputs used). The second pertains to whether perceptual equivalence can be concluded for MR of 3D stimuli, using a transfer-of-learning paradigm (i.e., perceptual equivalence is concluded when learning within-modalities is equal to transfer-of-learning between modalities). In relation to the third prediction, we briefly discuss the fit of RTs to rotation angles, when the MR task is performed with tactile input and with visual input, under switch and no-switch conditions. As they relate to our results, we address some explanatory factors for our results throughout the remainder of this section—as well as further research questions.

### MR response signatures

We observed the traditional MR response signatures in both perceptual modalities, in “[Session 1](#)” and “[Session 2](#)”. Participants’ errors and RTs increased with increasing rotation angle between objects, on parity-trials but not on non-parity-trials (Shepard and Metzler 1971). These result patterns indicate that MR was performed with both visual and tactile input. Our basic analyses of responses at higher rotation angles show that rotation angle effects tend to be more important for participants completing the visual task at baseline “[Session 1](#)” (see also “[Appendix A3](#)” correlational analyses). These analyses suggested that rotation angles (between objects) were not represented the same way, as the perceptual entry to the objects naturally differs for the tactile (contact sense) and visual (distance sense) inputs.

### Perceptual equivalence hypothesis and specific transfers of learning

For change rate analyses, differences in improvements between switch and no-switch conditions would be indicative of processing differences between MR with visual input and MR with tactile input. However, both our main analyses showed no effect of Switch (slope values), or only a close to significant effect of Switch (intercept values). We thus relied on *t* tests to assess whether learning in no-switch conditions and transfers of learning in

switch conditions were significantly different from zero. Only participants in no-switch groups and the prior visual switch group ( $V \rightarrow T$ ) significantly improved their slope and intercept values, in “[Session 2](#)”.

Participants in no-switch conditions showed the expected improvements in “[Session 2](#)” on all measures (including Accuracy and RTs, Heil et al. 1998; Toussaint et al. 2012). A different picture emerged, however, for participants’ performances in both switch conditions. Our RT results reflect those observed in previous studies that often show an absence of effect in the tactile to visual direction on spatial tasks (Behrmann and Ewell 2003; Garbin 1988; Hatwell 1983, 2000; Streri 2000). However, when individuals switched to the visual task in “[Session 2](#)”, informed by a tactile prior experience, they tended to be slower but more accurate (at least at higher rotation angles). In the other direction, a visual prior experience also showed tactile speed improvements, similar to improvements in no-switch conditions. Notably, faster speeds of MR with tactile input following a visual prior experience could suggest similar processing in MR with both perceptual inputs. However, when individuals switched to the tactile task in “[Session 2](#)”, informed by a visual prior experience, they also tended to be less accurate.

Overall, the results do not suggest (complete) perceptual equivalence for MR with 3D stimuli. Some transfer-of-learning effects were specific to the perceptual modality used in Session (1) These effects were also at odds with the characteristic learning demonstrated by the participants in no-switch groups. In this regard, basic perceptual differences seem unavoidable with 3D stimuli, as they could cause specific transfer-of-learning difficulties. However, this does not in and of itself rule out that participants recruit similar MR processes, independent of the sensory modality through which the rotated information is collected. The absence of tactile transfer-of-learning in the MR task with visual input could also suggest that tactile representations are just not useful (or too imprecise, see Rock and Victor 1964) when visual information is readily available in Session (2) Participants might judge the experience of touching very much different from seeing, although the underlying processes in both could very well be similar. Therefore, we cannot conclude beyond a doubt that the processes subtending MR of 3D stimuli are sensory-specific. Whether they are completely detached from the sensory modality through which shape information is collected is also still an open question. More research would be needed to disentangle these specific perceptual influences from the processes involved during MR of 3D stimuli. Notably, the presence or the absence of transfer-of-learning in this study could arise due to factors that we did not take into account.

## Strategic influences

It has been suggested that similar processes are active during MR of 2D stimuli with visual and tactile inputs (Prather and Sathian 2002), but we did not find complete evidence of this with 3D stimuli. We suggest that basic visual and tactile input differences could play-in the (seemingly) specific nature of the representations leading to a decision about parity-trials. Considering Fig. 2 (right panel) the tactile RT function for parity-trials also suggests a qualitative change of processing between trials with lower rotation angles ( $0^{\circ}$ – $60^{\circ}$ ) and those with higher rotation angles ( $90^{\circ}$ – $180^{\circ}$ ). In comparison, the visual RT function is parametrized by a smoothly rising slope. Conceivably, when participants' right hand grasps the misaligned comparison objects, at higher rotation angles, the perceptual analysis may require a different position of the hand, for the comparison to the model object to take place. This adjustment may be indicative of a specific (motor or body-centered) component for MR with tactile input.

Underlying mechanisms of visual and tactile 3D shape processing activate distinct functional paths and locations in the brain (Hsiao 2008). As such, a specific role of the somatosensory cortex has been observed during tactile 3D shape processing (Hsiao et al. 1996) and stimulus orientation processing (Hsiao et al. 2002). Tactile processing of 3D shape is also dependent on the position, structure and movement of hands (Johnson 2001), and inputs from different fingers (Klatzky et al. 1985; Pont et al. 1997) with afferent information drawing on cutaneous inputs and inputs from muscles and joints (Berryman et al. 2006). Whereas MR of 2D shapes has shown similar visual and tactile rotation angle effects on accuracy and RTs, with similar neuroimaging patterns (Prather et al. 2004; Sathian 2005), MR of 3D stimuli could comparatively tell a different story.

Perceiving 3D shape requires a very intricate tactile analysis, and accordingly we observed, on average, a time ratio difference of 5:1 s (tactile:visual) at all rotation angles. These time differences may point to strategic differences across modalities, and varying exploratory procedures (see Lederman and Klatzky 1987). As tactile procedures conceivably focus on sequential analyses of local object features, the opposite tendency of weighting global features has been observed for visual analysis (Lakatos and Marks 1999). In line with shape perception and MR, touch might therefore rely on the spatial processing of local cues (or directionality), whereas vision might rely on a more holistic process (vs. piecemeal process; see Kosslyn 1981; Dror et al. 1997) especially given the (meaningless) nature of the abstract 3D cube shapes used in our study (see Sharps and Nunes 2002; Smith and Dror 2001).

In a follow-up to this study, we conducted further analyses on exploratory procedures—specifically the number

of times participants shifted their attention between the model (left object) and rotated object (right object) (see Caissie 2013; Just and Carpenter 1985). For the tactile task, these averaged at 0.15 comparisons per second ( $\pm 0.06$ ). For the visual task, these averaged at 2.18 comparisons per second ( $\pm 0.71$ ), showing a significant Perceptual Modality effect,  $F(1,51) = 373.45$ ,  $p < .001$ ,  $\eta_p^2 = 0.88$ , with a significant rotation angle effect only in the visual modality,  $F(1,24) = 14.98$ ,  $p = .001$ ,  $\eta_p^2 = 0.88$  (tactile:  $F(1,27) = 0.83$ ,  $p = .371$ ,  $\eta_p^2 = 0.03$ ). These preliminary results also reflect a clear procedural difference when comparing participants' MR performances with tactile input and MR performances with visual input. Perhaps this distinction also has much to do with the specialization in tactile performances, and the seemingly difficult (or incomplete) transfer-of-learning between both perceptual modalities.

## Fit statistics and their meaning

In the baseline phase of the experiment, in “Session 1”, the mean curve across participants regressed to a linear function, independent of the perceptual modality. That the RTs fitted similarly well to the rotation angles were striking. This suggested a similar functional process involved in MR, with both perceptual inputs. However, the picture that emerged in “Session 2” showed stark differences in the trend lines. This suggests that with practice, different consolidation processes are at play within perceptual modalities (tactile vs. visual), which could lead to task specifications (e.g., rotation effects) that are not entirely overlapping (after a prior). In this regard, what practice informs is maybe different in nature, when comparing participants in both no-switch conditions. For participants in the visual no-switch condition, a strong linear effect remained evident in “Session 2”. Which was not the case for participants repeating the tactile task in “Session 2”. That the data regressed weakly to a linear model in one switch condition (T-V), and conversely to a more non-linear relationship in the other (V-T), also suggests a particular task specification following the switch. These results will certainly be worth exploring in more detail in future research (i.e., with different learning programs). Furthermore, RTs assumed a much larger variance in the tactile modality, which also suggests more diffused tactile solving strategies in MR. The explanatory factors underlying these individual differences also deserve further inquiry. Taken together, these results challenge the depiction of functionally equivalent/overlapping processing for both MR with tactile input and MR with visual input.

## Priming and speed-accuracy trade-offs in switching conditions

An alternative theoretical account not yet discussed is priming. Both sensory modalities (i.e., vision) can prime specific cognitive processes/strategies in the other (i.e., touch). At baseline, our analyses have shown slower tactile RTs compared to visual RTs, which mean that an extended window of temporal integration is necessary to mentally rotate tactile input successfully. Our analyses have also shown that participants influence their strategies (top-down) differently in both sensory contexts, for optimal integration of shape information and MR. Together with the fit analyses discussed, we can suggest that there are different task specifications and learning processes at play in MR with tactile input compared to MR with visual input. RTs to rotation angle relationships regress differently as a function of the participants' prior experience (visual or tactile) and the condition (switch or no-switch). Switching between modalities has thus shown difficult (re)integration of information (vs. learning in no-switch conditions), which we have taken as differences in sensory input and processes for MR. However, the possibility that task switching (or sensory switch) specifically primes a change in speed-accuracy trade-offs should also not be borne out (Liesefeld et al. 2015). By example, visual processing informs faster tactile speed (over accuracy), and conversely, tactile processing tends to inform a slower (more accurate) visual analysis (in comparison to baseline). Thus, processing differences in MR with tactile input and visual input might preferably be referred to as speed-accuracy trade-offs, or strategic differences, in disguise.

## Conclusion

In this study, we observed MR response signatures with both perceptual inputs (tactile and visual). However, learning between perceptual modalities was deemed under par when compared to learning within perceptual modalities. Preliminary model fit analyses (of the rotation angle effect on RTs) also suggested a different consolidation and specification in learning within perceptual conditions, and between perceptual conditions. In “[Session 1](#)”, that the RTs fitted similarly well to the rotation angles, for both types of perceptual responses, was striking. However, in “[Session 2](#)”, trend lines in the fitting analyses changed in a stark way when considering participants' responses, in the switch and tactile no-switch conditions. These results suggest that MR with 3D objects is not necessarily a perceptually equivalent process. Specialization (and priming) in exploration strategies might, however, be the main factor at play in these results—and not MR differences in and of themselves. More research is needed to determine whether transfer-of-learning

is specifically related to perceptual encoding (and MR) and to clearly define strategic (and individual) differences in a theoretically driven way (i.e., speed-accuracy trade-offs).

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## Appendix

See Table 1.

### A2: non-parity-trial analyses (accuracy and RTs “[Session 1](#)” and “[Session 2](#)”)

For “[Session 1](#)”, we ran single-factor ANOVAs comparing participants' responses as a function of Perceptual Modality (tactile vs. visual) on both Accuracy and RTs. The Accuracy analysis revealed a significant Perceptual Modality effect,  $F(1,53) = 6.26$ ,  $p = .016$ ,  $\eta_p^2 = 0.11$ . Participants' visual responses showed better Accuracy on non-parity-trials, compared to participants' tactile responses ( $91.5 \pm 13.4$  vs.  $83 \pm 19\%$ ). The RT analysis also revealed a significant Perceptual Modality effect,  $F(1,53) = 85.06$ ,  $p < .001$ ,  $\eta_p^2 = 0.62$ . As expected, participants in the tactile modality responded slower than participants in the visual modality ( $15.5 \pm 7.3$  vs.  $2.9 \pm 1.1$  s).

For “[Session 2](#)”, ANOVAs were based on Perceptual Modality (tactile vs. visual)  $\times$  2 Switch (switch vs. no-switch) for both Accuracy and RT analyses. The ANOVA on “[Session 2](#)” Accuracy only revealed a main effect of Perceptual Modality,  $F(1,51) = 5.36$ ,  $p = .025$ ,  $\eta_p^2 = 0.10$ , and a close to significant effect of Switch,  $F(1,51) = 3.58$ ,  $p = .064$ ,  $\eta_p^2 = 0.07$ . Overall, non-parity-trial responses with visual input are shown more accurate than non-parity-trial responses with tactile input ( $91.5 \pm 17.4$  vs.  $81.7 \pm 21\%$ ). Single variable ANOVAs carried out separately on tactile and visual response data revealed a close to significant Switch effect only for participants' tactile responses,  $F(1,26) = 3.94$ ,  $p = .058$ ,  $\eta_p^2 = 0.13$ . Participants in the switch condition tend to obtain significantly lower tactile accuracy compared to participants in the no-switch condition ( $75.8 \pm 21.8$  vs.  $87.7 \pm 18.4\%$ ). A visual prior experience is not necessarily beneficial for participants' tactile performances. The ANOVA on “[Session 2](#)” RTs only revealed a main effect of Perceptual Modality,  $F(1,51) = 103.97$ ,  $p < .001$ ,  $\eta_p^2 = 0.67$ , with the expected longer RTs with tactile input ( $10.6 \pm 3.7$  vs.  $2.9 \pm 1.2$  s). Single variable ANOVAs carried out separately on tactile and visual response data revealed a significant Switch effect only for participants' responses with visual input,  $F(1,26) = 3.94$ ,  $p = .058$ ,

$\eta_p^2 = 0.13$ . Participants in the visual switch condition thus show significantly longer RTs compared to participants in the visual no-switch condition ( $3.5 \pm 1.2$  vs.  $2.2 \pm 0.7$  s), which indicates that a tactile prior experience slows participants' visual responses in "Session 2".

### A3: accuracy and RT to rotation angle relationships for "Session 1" and "Session 2"

We examined the strength of the relationship between accuracy/RTs and rotation angle, for the participants' visual and tactile responses on parity-trials. For each participant we correlated the rotation angles (between object pairs) and Accuracy/RTs. For "Session 1", the participants' correlation coefficients (visual: mean  $r = -.27 \pm 0.22$ , tactile: mean  $r = -.10 \pm 0.16$ ) both differed significantly from zero—visual:  $t(26) = -6.35$ ,  $p < .001$ ,  $d = -1.73$ , tactile:  $t(27) = -3.47$ ,  $p = .002$ ,  $d = -0.93$ —for significantly linear effects. However, a paired  $t$  test comparing the two correlation sets was also significant,  $t(47.86) = -3.10$ ,  $p = .003$ , which suggests a stronger dependence of participants' accuracy on the rotation angle when considering responses with visual input, compared to responses with tactile input. For RTs, participants' correlation coefficients (visual: mean  $r = .46 \pm 0.18$ , tactile: mean  $r = .30 \pm 0.21$ ) both differed significantly from zero—visual:  $t(26) = 12.68$ ,  $p < .001$ ,  $d = 4.97$ , tactile:  $t(27) = 7.46$ ,  $p < .001$ ,  $d = 2.87$ —for the significantly linear effects. However, a paired  $t$  test comparing the two correlation sets was also significant,  $t(52.6) = 2.90$ ,  $p = .005$ , which suggests a stronger dependence of participants' RTs on rotation angle when considering responses with visual input, compared to responses with tactile input.

We further examined the strength of the relationship between accuracy/RTs and rotation angle in "Session 2", to mirror "Session 1" analyses. For accuracy, participants' correlation coefficients for participants in three groups— $V \rightarrow V$ : mean  $r = -.20 \pm 0.24$ ,  $T \rightarrow V$   $r = -.15 \pm 0.23$ ,  $V \rightarrow T$ : mean  $r = -.18 \pm 0.19$ —all differed significantly from zero,  $t_s(12,13) \geq -2.4$ ,  $p_s \leq 0.032$ ,  $d_s \geq -0.91$ , for the significantly linear effects. The correlation coefficient for the participants in the tactile no-switch group did not differ significantly from zero ( $T \rightarrow T$ : mean  $r = -.04 \pm 0.19$ ,  $t(13) = -0.8$ ,  $p = .418$ ,  $d = -0.32$ ). A paired  $t$  test comparing the correlation sets of tactile groups in "Session 2" ( $T \rightarrow T$  vs.  $V \rightarrow T$ ) almost reached significance,  $t(25.9) = 1.93$ ,  $p = .06$ . This result suggests a stronger dependence of RTs on rotation angle in the tactile switch condition, following a visual prior experience in "Session 1". Paired  $t$  tests comparing the correlation sets of groups  $T \rightarrow T$  to the visual groups,  $T \rightarrow V$  and  $V \rightarrow V$ , also failed to reach significance,  $t_s(25.2,24.9) \geq 1.3$ ,  $p_s \geq 0.07$ . For RTs, the correlation coefficients by groups— $V \rightarrow V$ : mean  $r = .50 \pm 0.20$ ,  $T \rightarrow V$   $r = .45 \pm 0.17$ ,  $T \rightarrow T$ : mean  $r = .27 \pm 0.17$ ,  $V \rightarrow T$ : mean  $r = .25 \pm 0.17$ —all

differed significantly from zero,  $t_s(12,13) \geq 4.00$ ,  $p_s \leq 0.002$ ,  $d_s \geq 1.51$ —for significant linearity effects. The difference between conditions (switch vs. no-switch) was not significant.

## References

- Amedi A, Malach R, Hendler T, Peled S, Zohary E (2001) Visuo-haptic object-related activation in the ventral visual pathway. *Nat Neurosci* 4:324–330
- Ballesteros S, Reales JM, Manga D (1999) Implicit and explicit memory for familiar and novel objects presented to touch. *Psichotema* 11:785–800
- Barquero B, Logie RH (1999) Imagery constraints on quantitative and qualitative aspects of mental synthesis. *Eur J Cogn Psychol* 11:315–333
- Behrmann M, Ewell C (2003) Expertise in tactile pattern recognition. *Psychol Sci* 14:480–486
- Berryman LJ, Yau JM, Hsiao SS (2006) Representation of object size in the somatosensory system. *J Neurophysiol* 96:27–39
- Bethell-Fox CE, Shepard RN (1988) Mental rotation: effects of stimulus complexity and familiarity. *J Exp Psychol Hum* 14:12–23
- Biederman I (1987) Recognition-by-components: a theory of human image understanding. *Psychol Rev* 94:115–117
- Caissie AF (2013) Etude des transferts intermodaux lors de tâche de rotation mentale. Presses Académiques Francophones, Saarbrücken
- Caissie A, Vigneau F, Bors D (2009) What does the mental rotation test measure? An analysis of item difficulty and item characteristics. *Op Psychol J* 2:94–102
- Carpenter PA, Eisenberg P (1978) Mental rotation and the frame of reference in blind and sighted individuals. *Percept Psychophys* 23:117–124
- Cohen DJ, Blair C (1998) Mental rotation and temporal contingencies. *J Exp Anal Behav* 70:203–214
- Cohen MS, Kosslyn SM, Breiter HC, DiGirolamo GJ (1996) Changes in cortical activity during mental rotation: a mapping study using functional MRI. *Brain J Neurol* 119:89–100
- Cooper L (1975) Mental rotation of random two-dimensional shapes. *Cogn Psychol* 7:20–43
- Corballis MC, McMaster H (1996) The roles of stimulus-response compatibility and mental rotation in mirror-image and left-right decisions. *Can J Exp Psychol* 50:397–401
- Dalecki M, Hoffmann U, Bock O (2012) Mental rotation of letters, body parts and complex scenes: separate or common mechanisms? *Hum Mov Sci* 31:1151–1160
- Dellantonio A, Spagnolo F (1990) Mental rotation of tactual stimuli. *Acta Psychol* 73:245–257
- Dror IE, Kosslyn SM (1994) Mental imagery and aging. *Psychol Aging* 9:90–102
- Dror I, Ivey C, Rogus C (1997) Visual mental rotation of possible and impossible objects. *Psychon Bull Rev* 4:242–247
- Easton RD, Greene AJ, Srinivas K (1997) Transfer between vision and haptics: memory for 2-D patterns and 3-D objects. *Psychon Bull Rev* 4:403–410
- Farah MJ (1988) Is visual imagery really visual? Overlooked evidence from neuropsychology. *Psychol Rev* 95:307–317
- Farah MJ, Hammond KM, Levine DN, Calvanio R (1988) Visual and spatial mental imagery: dissociable systems of representation. *Cogn Psychol* 20:439–462
- Finke RA, Shepard RN (1986) Visual functions of mental imagery. In: Boff KR, Kaufman L, Thomas JP (eds) *Handbook of perception and human performance*. Wiley-Interscience, New York, pp 37–55

- Garbin CP (1988) Visual-haptic perceptual nonequivalence for shape information and its impact upon cross-modal performance. *J Exp Psychol Hum* 14:547–553
- Garbin CP (1990) Visual-touch perceptual equivalence for shape information in children and adults. *Percept Psychophys* 48:271–279
- Garbin CP, Bernstein IH (1984) Visual and haptic perception of three-dimensional solid forms. *Percept Psychophys* 36:104–110
- Hatwell Y (1983) The effects of previous visual experience on haptic performances of sighted and blind children. In: Horn E (ed) *Multimodal convergence in sensory systems*. Gustav Fischer Verlag, Stuttgart and New York, pp 325–333
- Hatwell Y (2000) Les coordinations intermodales chez l'enfant et l'adulte. In Hatwell Y, Streri A, Gentaz E (eds), *Toucher pour connaître: psychologie cognitive de la perception tactile manuelle* (pp 211–224). Paris: Presses universitaires de France
- Heil M, Rösler F, Link M, Bajric J (1998) What is improved if a mental rotation task is repeated—the efficiency of memory access, or the speed of a transformation routine? *Psychol Res* 61:99–106
- Hsiao S (2008) Central mechanisms of tactile shape perception. *Curr Opin Neurobiol* 18:418–424
- Hsiao SS, Johnson KO, Twombly IA, DiCarlo JJ (1996) Form processing and attention effects in the somatosensory system. In: Franzen O, Johansson RS, Terenius L (eds) *Somesthesia and the Neurobiology of the Somatosensory Cortex*. Birkhäuser, Basel, pp 229–247
- Hsiao S, Lane J, Fitzgerald P (2002) Representation of orientation in the somatosensory system. *Behav Brain Res* 135:93–103
- James TW, James KH, Humphrey GK, Goodale MA (2006) Do visual and tactile object representations share the same neural substrate? In: Heller MA, Ballesteros S (eds) *Touch and blindness: psychology and neuroscience*. Lawrence Erlbaum Associates Publishers, Mahwah, pp 139–155
- Johnson K (2001) The roles and functions of cutaneous mechanoreceptors. *Curr Opin Neurobiol* 11:455–461
- Just M, Carpenter P (1985) Cognitive coordinate systems: accounts of mental rotation and individual differences in spatial ability. *Psychol Rev* 92:137–172
- Kawamichi H, Kikuchi Y, Ueno S (2007) Spatio-temporal brain activity related to rotation method during a mental rotation task of three-dimensional objects: an MEG study. *Neuroimage* 37:956–965
- Klatzky R, Lederman S, Metzger V (1985) Identifying objects by touch: an expert system. *Percept Psychophys* 37:299–302
- Kosslyn S (1981) The medium and the message in mental imagery: a theory. *Psychol Rev* 88:46–66
- Kosslyn SM, DiGirolamo GJ, Thompson WL, Alpert NM (1998) Mental rotation of objects versus hands: neural mechanisms revealed by positron emission tomography. *Psychophysiol* 35:151–161
- Kosslyn SM, Thompson WL, Ganis G (2006) *The case for mental imagery*. Oxford University Press, New York
- Kozhevnikov M, Kosslyn S, Shepard J (2005) Spatial versus object visualizers: a new characterization of visual cognitive style. *Mem Cognit* 33:710–726
- Lackner JR, DiZio P (2005) Vestibular, proprioceptive, and haptic contributions to spatial orientation. *Annu Rev Psychol* 56:115–147
- Lakatos S, Marks L (1999) Haptic form perception: relative salience of local and global features. *Percept Psychophys* 61:895–908
- Lederman S, Klatzky R (1987) Hand movements: a window into haptic object recognition. *Cogn Psychol* 19:342–368
- Liesefeld HR, Zimmer HD (2013) Think spatial: the representation in mental rotation is nonvisual. *J Exp Psychol Learn* 39:167–182
- Liesefeld HR, Fu X, Zimmer HD (2015) Fast and careless or careful and slow? Apparent holistic processing in mental rotation is explained by speed-accuracy trade-offs. *J Exp Psychol Learn* 41:1140–1151
- Logie RH, Helstrup T (1999) Introduction. *Eur J Cogn Psychol* 11:289–294
- Millar S (2006) Processing spatial information from touch and movement: implications from and for neuroscience. In: Heller MA, Ballesteros S (eds) *Touch and blindness: psychology and neuroscience*. Lawrence Erlbaum Associates Publishers, Mahwah, pp 25–48
- Millar S, Al-Attar Z (2002) The Müller-Lyer illusion in touch and vision: implications for multisensory processes. *Percept Psychophys* 64:353–365
- Pascual-Leone A, Hamilton RH (2001) The metamodal organization of the brain. *Prog Brain Res* 134:427–445
- Pont S, Kappers A, Koenderink J (1997) Haptic curvature discrimination at several regions of the hand. *Percept Psychophys* 59:1225–1240
- Prather SC, Sathian K (2002) Mental rotation of tactile stimuli. *Cogn Brain Res* 14:91–98
- Prather SC, Votaw JR, Sathian K (2004) Task-specific recruitment of dorsal and ventral visual areas during tactile perception. *Neuropsychologia* 42:1079–1087
- Provost A, Johnson B, Karayanidis F, Brown S, Heathcote A (2013) Two routes to expertise in mental rotation. *Cogn Sci* 37:1321–1342
- Pylyshyn Z (1979) The rate of “mental rotation” of images: a test of a holistic analogue hypothesis. *Mem Cogn* 7:19–28
- Pylyshyn ZW (2003) *Seeing and visualizing: it's not what you think*. MIT Press, Cambridge
- Reales JM, Ballesteros S (1999) Implicit and explicit memory for visual and haptic objects: cross-modal priming depends on structural descriptions. *J Exp Psychol Learn* 25:644–663
- Revesz G (1950) *Psychology and the art of the blind* (Trad. H. A. Wolff). Longmans Green, London
- Rock I, Victor J (1964) Vision and touch: an experimentally created conflict between the two senses. *Sci* 143:594–596
- Röder B, Rösler F, Hennighausen E (1997) Different cortical activation patterns in blind and sighted humans during encoding and transformation of haptic images. *Psychophysiol* 34:292–307
- Roland PE, Gulyás B (1994) Visual imagery and visual representation. *Trends Neurosci* 17:281–287
- Rösler F, Röder B, Heil M, Hennighausen E (1993) Topographic differences of slow event-related brain potentials in blind and sighted adult human participants during haptic mental rotation. *Cogn Brain Res* 1:145–159
- Sathian K (2005) Visual cortical activity during tactile perception in the sighted and the visually deprived. *Dev Psychobiol* 46:279–286
- Sharps MJ, Nunes MA (2002) Gestalt and feature-intensive processing: toward a unified model of human information processing. *Curr Psychol Dev Learn Personal Soc* 21:68–84
- Shepard R, Cooper L (1982) *Mental images and their transformations*. MIT Press, Cambridge
- Shepard RN, Metzler J (1971) Mental rotation of three-dimensional objects. *Science* 171:701–703
- Shepard S, Metzler D (1988) Mental rotation: effects of dimensionality of objects and type of task. *J Exp Psychol Hum* 14:3–11
- Smith W, Dror IE (2001) The role of meaning and familiarity in mental transformations. *Psychon Bull Rev* 8:732–741
- Stigler J, Nusbaum H, Chalip L (1988) Developmental changes in speed of processing: central limiting mechanism or skill transfer? *Child Dev* 59:1144
- Streri A (2000) Les coordinations intermodales chez le bébé. In Hatwell Y, Streri A et Gentaz E (eds), *Toucher pour connaître: psychologie cognitive de la perception tactile manuelle* (pp 193–209). Paris: Presses universitaires de France
- Tagaris GA, Richter W, Kim SG, Pellizzer G, Andersen P, Ugurbil K et al (1998) Functional magnetic resonance imaging of mental rotation and memory scanning: a multidimensional scaling analysis of brain activation patterns. *Brain Res Rev* 26:106–112

- Tarr M, Pinker S (1989) Mental rotation and orientation-dependence in shape recognition. *Cogn Psychol* 21:233–282
- Tippet L (1992) The generation of visual images: a review of neuropsychological research and theory. *Psychol Bull* 112:415–432
- Toussaint L, Caissie A, Blandin Y (2012) Does spatial ability depend on sensory-specific experience? *J Cogn Psychol* 24(4):387–394
- Treisman A, Gormican S (1988) Feature analysis in early vision: evidence from search asymmetries. *Psychol Rev* 95:15–48
- Vandenberg S, Kuse A (1978) Mental rotations, a group test of three-dimensional spatial visualization. *Percept Mot Skills* 47(2):599–604
- Volcic R, Wijntjes MWA, Kappers AML (2009) Haptic mental rotation revisited: multiple reference frame dependence. *Acta Psychol* 130(3):251–259
- Volcic R, Wijntjes MWA, Kool EC, Kappers AML (2010) Cross-modal visuo-haptic mental rotation: comparing objects between senses. *Exp Brain Res* 203:621–627
- Wallace B, Hofelich B (1992) Process generalization and the prediction of performance on mental imagery tasks. *Mem Cogn* 20:695–704
- World Medical Association (2013) World Medical Association Declaration of Helsinki: ethical principles for medical research involving human subjects. *JAMA* 310:2191–2194
- Wraga M, Shephard JM, Church JA, Inati S, Kosslyn SM (2005) Imagined rotations of self versus objects: an fMRI study. *Neuropsychologia* 43:1351–1361
- Zhang M, Weisser VD, Stilla R, Prather SC, Sathian K (2004) Multisensory cortical processing of object shape and its relation to mental imagery. *Cogn Affect Behav Neuro* 4:251–259