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Tactile recognition of visual stimuli: Specificity versus generalization of perceptual learning

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ABSTRACT

Sensory substitution devices aim at assisting a deficient sensory modality by means of another sensory modality. For instance, to perceive with visual-to-tactile devices, users learn to recognize visual stimuli through their tactile conversion. A crucial characteristic of learning lies in the ability to generalize, that is, the ability to extend the acquired perceptual abilities to both new stimuli and new perceptual conditions. The study reported here investigated the perceptual learning of tactile alphanumeric stimuli. The learning protocol consisted in alternating a repeated list of symbols with lists of new symbols. A first experiment revealed that, when each list consisted of 4 stimuli, recognition performance improved over time only for the repeated list. This result suggests that learning a small set of stimuli involves stimulus-specific learning strategies, preventing generalization. A second experiment revealed that increasing to six the set of learned stimuli results in higher generalization abilities. This result can be explained by greater difficulties in using stimulus-specific strategies in this case, thereby favouring the use of generalization strategies. Feature variability also appeared to be important to achieve generalization. Thus, as in visual perceptual learning, the involvement of stimulus-specific versus general strategies depends on task difficulty and feature variability. A third experiment highlighted that tactile perceptual learning generalizes to changes in orientation. These results are discussed in terms of brain plasticity as they influence the design of learning methods for using sensory substitution devices, with the aim to compensate visual impairments.

1. Introduction

Perceptual learning, defined as the performance improvement in perceptual tasks resulting from training (Fahle & Poggio, 2002), reveals the plasticity of humans' sensory systems. Sensory substitution is an illustrative example for which perceptual learning and plasticity play a crucial role. Sensory substitution devices aim at assisting a deficient sensory modality (e.g., vision) by means of another sensory modality (e.g., audition or touch; see Auvray & Myin, 2009, for a review). Even if the question of whether sensory substitution genuinely restores vision to their users is highly debatable, this technique provides a new way to receive sensory information from the environment. Brain plasticity allows users to have access to information in a novel way. For instance, after training with a visual-to-tactile conversion device, the tactile stimulation, initially felt on the surface of the skin, is attributed to external objects (Hartcher-O'Brien & Auvray, 2014).

Numerous studies have reported that sensory substitution devices enable blind and blindfolded sighted people to localize (e.g., Levy-Tzedek, Hanassy, Abboud, Maidenbaum, & Amedi, 2012; Renier et al.,

2005) and recognize simple shapes or complex objects (e.g., Arno et al., 2001; Auvray, Hanneton, & O'Regan, 2007; Pollok, Schnitzler, Mierdorf, Stoerig, & Schnitzler, 2005; Sampaio, Maris, & Bach-y-Rita, 2001). Most users are able, in one or two hours, to approximate objects' location and shape. However, to gain precision in these tasks and to perform more complex ones, a more intensive training is required. The length of the training is estimated at around eight hours with visual-to-tactile devices (Kaczmarek & Haase, 2003) and 10–15 with visual-to-auditory devices (Auvray, Hanneton, & O'Regan, 2007). It would be even more important to achieve a high level of expertise, for instance to be able to recognize facial expressions (Striem-Amit, Guendelman, & Amedi, 2012).

A crucial characteristic of learning lies in the ability to generalize, that is, to extend the acquired perceptual abilities to both new stimuli and new perceptual conditions. For instance, in the case of learning a sensory substitution device, generalization enables their users, trained in specific conditions and with specific shapes and objects, to extract the rules underlying perception with the device and to apply them to new objects or to previously learned objects perceived in new

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conditions. In other words, users do not simply associate visual stimuli to their auditory or tactile conversion, but they become able to extract the perceptual characteristics of a scene and of their constituting objects and then they are able to transfer this learning to new scenes and objects.

Studies have reported contrasting results regarding specificity versus generalization of perceptual learning (see [Fahle, 2005](#), for a review). For instance, visual perceptual learning can be highly specific to retinal position, object orientation, and object shape (e.g., [Sigman & Gilbert, 2000](#); [Yi, Olson, & Chun, 2006](#)). Tactile perceptual learning has also been reported to be specific to the trained body surface, with a transfer of learning restricted to adjacent or homologous contralateral surfaces (e.g., [Harrar, Spence, & Makin, 2014](#); [Sathian & Zangaladze, 1997](#)). On the other hand, studies have reported generalization of learning. For instance, [Furmanski and Engel \(2000\)](#) have found object-specific but size-invariant perceptual learning in visual object recognition. Perceptual learning has also been reported to transfer to non-adjacent body surfaces in tactile recognition of alphanumerical symbols ([Arnold & Auvray, 2014](#)).

The reverse hierarchy theory (RHT) of perceptual learning ([Ahissar & Hochstein, 2004](#)) has been proposed to account for these discrepant results. According to this theory, the degree of specificity depends on the difficulty of the perceptual task and on the level of cortical processing that is required to perform the task. For a difficult task, involving low-level cortical processes that are highly specific to the characteristics of the task (e.g., fine discrimination of visual orientations), perceptual learning is specific to the characteristics of the task (e.g., the visual orientations that have been discriminated) and it does not generalize to new characteristics (e.g., new orientations). On the other hand, for an easier task, involving higher-level processing, perceptual learning is less specific to the low-level characteristics of the task or of the stimuli. Task difficulty, either during the learning phase or during the evaluation of generalization, has indeed been reported to influence both the specificity and generalization of learning ([Jeter, Doshier, Petrov, & Lu, 2009](#); [Liu & Weinsall, 2000](#); [Wang, Zhou, & Liu, 2013](#)). Note however that, in some cases, generalization turns out to be easier with a difficult task than with an easy one ([Liu & Weinsall, 2000](#)). Other factors than task difficulty can play a role in influencing specificity versus generalization of learning. For instance, the variability of the learned stimuli contributes to generalization ([Hussain, Bennett, & Sekuler, 2012](#)). On the other hand, a long duration of the learning phase contributes to specificity ([Jeter, Doshier, Liu, & Lu, 2010](#)), possibly due to sensory adaptation ([Harris, Glikhsberg, & Sagi, 2012](#)).

Perceptual learning can also transfer from one sensory modality to another. For instance, learning to discriminate tactile intervals has been reported to transfer to the auditory sensory modality ([Nagarajan, Blake, Wright, Byl, & Merzenich, 1998](#)). Based on the RHT ([Ahissar & Hochstein, 2004](#)), [Proulx, Brown, Pasqualotto, and Meijer \(2014\)](#) made the hypothesis that the broad brain activation of multisensory processing reinforces generalization of learning, especially because multisensory processing involves high-level multimodal brain areas. Sensory substitution, by converting the information from one sensory modality into another, is thus an ideal candidate for observing general perceptual learning. In this field of research, [Kim and Zatorre \(2008\)](#) found that learning to recognize simple shapes and complex objects with a visual-to-auditory conversion device generalizes to new objects. This result was then reproduced with tactile-to-auditory conversion of shapes ([Kim & Zatorre, 2010](#)). Learning complex stimuli, corresponding to the auditory conversion of visual shapes, has also been reported to involve faster perceptual learning and greater amplitude of generalization to new stimuli than what occurred when learning simple stimuli ([Brown & Proulx, 2013](#)). Similarly [Auvray et al., 2007](#); see also [Auvray, 2004](#), for more details) found that learning every-day life objects transfers to some extent to the recognition of different objects belonging to the same category. Generalization to new stimuli with even more complex objects such as facial expressions has also been reported to occur

([Striem-Amit et al., 2012](#)). Finally, sensory-motor learning with a visual-to-auditory device has been reported to transfer across sensory modalities ([Levy-Tzedek, Novick et al., 2012](#)). However, if few studies have investigated the generalization of learning with visual-to-auditory devices, no study to date has investigated the generalization of learning during the use of a visual-to-tactile device.

The study reported here aims at evaluating whether learning to recognize tactile conversion of visual stimuli generalizes to new stimuli and to new perceptual conditions. The methodology is based on a recognition task of alphanumerical symbols presented on the participants' stomach by means of sequences of vibrotactile stimulations. Alphanumerical symbols are usually perceived visually, and rarely by touch. Thus the tactile recognition task requires training, similarly to what occurs when learning to use a visual-to-tactile substitution device. A similar task was previously used to show that learning to recognize tactile symbols transfers from trained to untrained body surfaces ([Arnold & Auvray, 2014](#)). In the present study, the tactile symbols were presented on the stomach as, for visual-to-tactile sensory substitution devices, this body part presents a good compromise between the size of the skin surface and its spatial resolution (see [Haggard, Taylor-Clarke, & Kennett, 2003](#), for spatial resolution of the different body surfaces). In addition, it is central on the body and, contrary to the hand, its position and orientation relative to the rest of the body does not change much. Finally, contrary to body surfaces with greater spatial resolution, in particular the fingertips and the tongue, the stomach is rarely used for everyday tactile perception (e.g., haptic object recognition) and it can thus be used for receiving additional tactile information without disturbing people's usual perception and action.

In the first two experiments reported here, the role of stimulus variability in the ability to generalize to new symbols during learning was evaluated by comparing the learning of sets of four symbols (Experiment 1; low variability) to the learning of sets of six symbols (Experiment 2; high variability). If stimulus variability influences the stimulus-specific versus generalized learning strategies, generalization should be better with high than with low stimulus variability. In the third experiment, the ability to generalize to new orientations was evaluated. Orientation is an important source of perceptual variability and changes in orientation frequently disturb the recognition of objects that are learned visually (e.g., [Arnold & Siéhoff, 2012](#)) or by touch (e.g., [Newell, Ernst, Tjan, & Bühlhoff, 2001](#)).

2. Experiment 1

Experiment 1 was designed to investigate whether learning to recognize tactile symbols generalizes to new symbols when learning a limited number of symbols. In order to investigate generalization to new symbols, a similar procedure to the one used by [Dutilh, Krypotos, and Wagenmakers \(2011\)](#) was used. It consists in alternating blocks with a repeated list of stimuli and blocks with new lists of stimuli. If stimulus-specific learning is involved, recognition performance should increase with practice (i.e., across blocks) only for repeated stimuli. In contrast, if generalized learning is involved, recognition performance should increase for both repeated and new stimuli.

The second aim of this experiment was to investigate whether the generalization of learning depends on the spatial perspective that is naturally adopted when interpreting tactile information presented on the body. Using the graphesthesia task, which consists in recognizing ambiguous asymmetrical symbols presented on the body surface (e.g., the letters b, d, p, and q), previous studies have shown that some observers prefer to adopt a self-centred spatial perspective (i.e., centred on the observer's body) whereas others prefer to adopt a decentred one (i.e., centred on a location different from that of the observer) (see [Arnold, Spence, & Auvray, in press](#), for a review). These individual differences have been reported to reflect the existence of a natural perspective rather than being due to an arbitrary choice ([Arnold, Spence, & Auvray, 2016](#)). Moreover, decentred observers are better at

adopting an unnatural perspective than self-centred observers are. Thus, this experiment also investigated whether this superiority of naturally decentred observers over naturally self-centred ones is specific to the adoption of spatial perspectives or whether it reflects a general ease to interpret tactile information instead. When tactile stimuli are presented on people's stomach, three perspectives can be adopted, one decentred and two self-centred (trunk-centred or head-centred). In the present experiment, only those participants that naturally adopt a trunk-centred or a decentred perspective were tested.

2.1. Material and methods

2.1.1. Participants

Two hundred and fifty-five participants (154 females and 101 males; mean age = 25.2 years, range = 18–47 years; 30 participants were left-handed and 225 participants were right-handed) were initially recruited via mailing lists to participate in 6 different experiments (i.e., the 3 experiments reported in the present study and 3 experiments investigating different research questions reported in different studies). In all these experiments, the graphesthesia task was used to investigate the participants' spatial perspectives. The participants were randomly allocated to one of these 6 experiments in order to generate groups based upon natural perspective. Five participants were excluded from the set of experiments because their natural perspective could not be correctly identified. For the 250 remaining participants, 49.6% adopted a trunk-centred perspective, 29.2% a head-centred perspective, and 21.2% a decentred perspective. For the present study, 20 trunk-centred and 20 decentred participants were included in Experiment 1, 32 trunk-centred participants in Experiment 2, and 24 trunk-centred participants in Experiment 3.

Forty participants completed the present experiment (25 females and 15 males; mean age = 24.8 years, range = 18–41 years; three participants were left-handed and 37 participants were right-handed). Half of the participants (14 females and 6 males; mean age = 24.4 years, range = 18–41 years) had a natural trunk-centred perspective and the other half (11 females and 9 males; mean age = 25.2 years, range = 20–33 years) had a natural decentred perspective. All the participants were naive to the purpose of the experiment. Participants provided their informed consent and received payment for their participation. The experiment took approximately one hour to complete and was performed in accordance with the ethical standards laid down in the [Declaration of Helsinki \(1991\)](#).

2.1.2. Apparatus

The tactile stimuli were presented by means of 9 rectangular vibrators (Haptuator Mark II, Tactile Labs, Montreal, Canada) arranged in a 3-by-3 array with a centre-to-centre spacing of 5 cm (see [Fig. 1a](#)). Each vibrator measured 0.9 cm vertically by 3.2 cm horizontally for a total surface area of 10.9 cm vertically by 13.2 cm horizontally. A nine-channel amplifier drove each vibrator independently at a 250-Hz frequency. The vibrator array was placed on the participants' stomach, above their clothes, by means of an elastic belt. The vibrator array was placed symmetrically to their body mid-sagittal line, with the 3 lower vibrators located above the waist. Only one layer of clothing was allowed between the skin and the vibrators. The participants individually selected the intensity of each vibrator by means of an adjustment method.

Instructions and feedback were presented on a 23-inch screen with a 1920 × 1080 resolution. The participants wore noise-reducing headphones with a noise reduction rating of 30 dB, in order to mask any sounds made by the vibrators.

2.1.3. Stimuli

Twenty asymmetrical symbols were presented on the participants' stomach: the uppercase letters B, C, D, E, F, G, J, K, L, N, P, Q, R, and Z and the numbers 1, 2, 3, 4, 5, and 6. The use of asymmetrical symbols

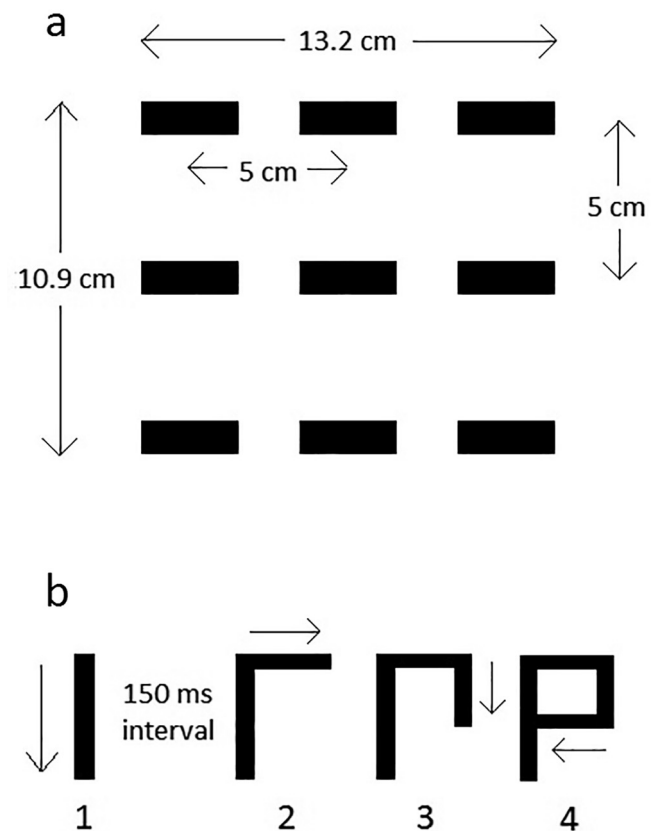


Fig. 1. Illustration of the drawing of alphanumerical symbols with the 3-by-3 vibrotactile matrix. (a) Schematic figure illustrating the vibrotactile matrix. (b) The sequence of vibrations chosen for drawing the letter P.

allowed presenting the symbols according to either trunk-centred or decentred perspectives. According to the trunk-centred perspective, the left and right of the symbols were congruent to participants' left-right axis. According to the decentred perspective, the left and right were opposite to participants' left-right axis. The top and bottom of the symbols were congruent to participants' top-bottom axis for both the trunk-centred and decentred perspectives.

The symbols were traced with sequences of vibrotactile stimulations mapping the trajectory of manual drawing (see [Arnold & Auvray, 2014](#), for more details). Each vibrator composing the sequence was activated for 250 ms and there were 150 ms intervals between two consecutive vibrations that were spatiotemporally discontinuous (e.g., the end of the vertical descending stroke and the beginning of the loop of the letter P; see [Fig. 1b](#)). This interval avoids possible errors of interpretation caused by an irrelevant grouping of vibrations. The participants were instructed that these temporal intervals corresponded to a spatial discontinuity in manual letter drawing. It should be underlined that with such a device, the symbols' drawings do not exactly match manual drawing, as curved features are not possible and thus they are replaced by right-angled features. Tactile recognition of alphanumerical symbols has nonetheless previously been reported to be successful with the use of a similar 3-by-3 vibrotactile matrix ([Yanagida, Kakita, Lindeman, Kume, & Tetsutani, 2004](#)). The mean duration of symbols was 2215 ms (SD = 618). Five lists of four symbols were created with similar mean durations (List1: PQZ5, 2363 ms; List2: JK36, 2175 ms; List3: FLR4, 2063 ms; List4: BCD2, 2263 ms; EGN1, 2213 ms). Each of these lists was composed of three letters and one number except List2, which was composed of two letters, and two numbers.

In addition, the four ambiguous lowercase letters b, d, p, and q were used for the identification of each participant's natural perspective. The letters were traced beginning from the stem and ending with the loop,

with a sequence of eight 250 ms vibrations without intervals between each vibration.

2.1.4. Procedure

The first part of the experiment was designed to identify each participant's natural perspective. The participants sat in front of the computer screen. On each trial, one of the four possible ambiguous letters (b, d, p, and q) was displayed on the participants' stomach. The participants were instructed to report the letter they perceived as spontaneously as possible by pressing the corresponding key with the index finger of their dominant hand. They were informed that each vibrotactile sequence could be interpreted as one of the four letters, depending on how they assign the left–right and top–bottom axes of the letter, and that there were consequently no correct or incorrect responses. The participants were asked to report their responses as fast as possible. They completed one block of 16 trials (four trials for each of the four letters). If no clear preference for adopting one of the perspectives was identified in the first block, the participants completed additional blocks until their natural perspective could be clearly identified, without exceeding six blocks. Only one block was required for 24 participants, two blocks for 12 participants, and three blocks for four participants. There are three possible causes for this individual variability that can occur individually or in combination. First, the natural perspective may emerge faster for some participants over others. Second, some people might not have a natural perspective. Third, some participants may have had difficulties to understand the instructions, leading them to adopt the most 'logical' perspective (i.e., the experimenter's perspective) rather than the easiest perspective for them.

The second part of the experiment was designed to investigate participants' abilities to recognize unambiguous asymmetrical symbols. On each trial, one symbol was presented on the participants' stomach. The participants were instructed to report which symbol was presented by pressing the corresponding key with the index finger of their dominant hand. Rather than using the real position of each letter and number on the computer keyboard, stickers with the four symbols used in each list written on it were placed on four adjacent keys on the keyboard. The keyboard was located in front of the participants, slightly shifted toward the left for left-handed participants or to the right for right-handed participants. In this part of the experiment, the participants were informed that the symbols would be presented according to their natural perspective and that there were correct and incorrect responses. The participants were asked to give their responses as accurately as possible. Response times (RTs) were recorded as a secondary measure of performance but emphasis was put on accuracy (see [Supplementary material](#) for the analyses of RTs). The participants were able to give their responses at any time from the onset of the first vibration and up to 3000 ms after the end of the last vibration (at which point the trial was terminated). At the end of each trial, there was an interval of 3000 ms before the beginning of the next trial.

The participants completed eight blocks of trials for the recognition task. In each block, one of the five lists was presented. One of the lists (the repeated list; labelled A) was presented four times. The other four lists (new lists; labelled B through E) were presented once each. Thus there were four blocks with the repeated list and four blocks with the new lists, which were alternated as follows: ABACADAE for half of the participants and BACADAEA for the other half. Note that each of the five lists served as the repeated list for a fifth of the participants ($N = 16$). In addition, each list was presented the same number of times across participants as lists B, C, D, and E.

Each block consisted of 40 trials (10 presentations of each symbol). At the end of each block of trials, global feedback indicating the percentage of correct responses and the mean RT was given. The participants had a short pause between each block. At the beginning of each block, the participants were given four practice trials (one trial for each symbol). In this practice block, feedback was given at the end of each trial: the correct answer was visually displayed on the computer screen

once the participants responded.

2.2. Results

Trials in which the participants failed to make a response before the trial was terminated (0.56% of trials) were not included in the data analyses. The accuracy of symbol recognition was measured by the percentage of correct responses in each condition. An ANOVA was conducted with Type of list (repeated, new) and Block (block 1, block 2, block 3, block 4) as within-participant factors and with Natural perspective (trunk-centred, decentred) as a between-participant factor. As there was no significant effect of Gender and no interaction between Gender and any of the other factors (in this experiment as well as in Experiments 2 and 3), this factor was not included in the reported analyses.

There was a significant effect of Block, $F(3,114) = 3.46$, $p < .05$, and a significant interaction between Block and Type of list, $F(3,114) = 5.40$, $p < .01$, showing an increase in accuracy across blocks for the repeated list (block 1 = 91.2%, SD = 9.4; block 2 = 94.1%, SD = 7.2; block 3 = 96.4, SD = 5.7; block 4 = 97.6, SD = 2.6) but not for the new lists (block 1 = 92.4%, SD = 8.8; block 2 = 91.3%, SD = 10.3; block 3 = 93.1, SD = 7.3; block 4 = 92.0, SD = 7.6) (see [Fig. 2](#)). The linear trend test was significant for the repeated list, $F(1,38) = 23.17$, $p < .001$, but not for the new lists, $F(1,38) < 1$. There was also a significant effect of Type of list, $F(1,38) = 13.59$, $p < .001$, with greater accuracy for repeated (94.8%, SD = 7.1) than for new lists (92.2%, SD = 8.6). Finally, the three-way interaction between Natural perspective, Type of list, and Block almost reached significance, $F(3,114) = 2.56$, $p = .058$. However, the analysis of this interaction revealed no difference between trunk-centred and decentred participants in generalization of learning as the linear trend tests revealed significant increase in accuracy across blocks for the repeated list but not for the new lists for the two groups (repeated list: $F(1,38) = 11.79$, $p < .01$, for trunk-centred, $F(1,38) = 11.38$, $p < .01$, for decentred; new lists: $F(1,38) < 1$, for both trunk-centred and decentred).

The number of blocks required to identify the participants' natural perspective individually varied. This might indicate either that the adopted perspective is more or less natural or that the natural perspective emerges faster for some participants over others. This variability was taken into account in order to further investigate the influence of natural perspective on learning and generalization. More specifically, the participants who required only one block of ambiguous symbols ($N = 24$) were compared with the participants who required

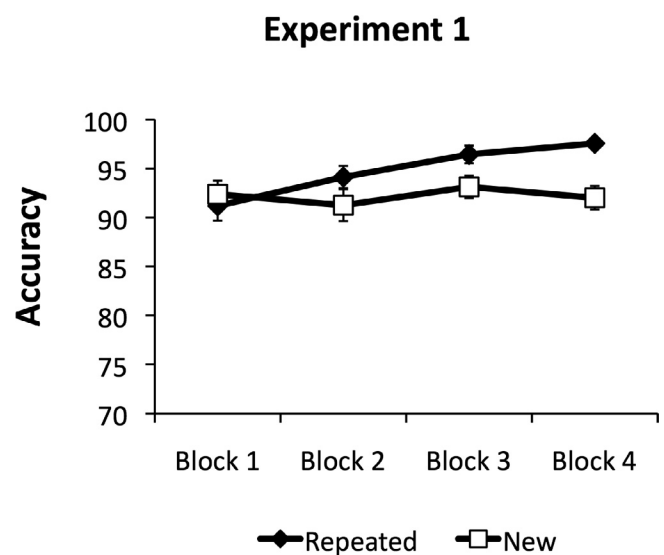


Fig. 2. Participants' accuracy during Experiment 1 as a function of Type of List (repeated, new) and Block. Error bars represent the standard errors of the means.

several blocks (i.e., two or three blocks; $N = 16$). An ANOVA was conducted with Number of blocks (one, several) as a between-participant factor and with Type of list (repeated, new) and Blocks (block 1, block 2, block 3, block 4) as within-participant factors. The results revealed a significant effect of Number of blocks, $F(1,38) = 6.73$, $p < .05$, with greater accuracy for participants with one block (95.0%, $SD = 3.3$) than for participants with several blocks (91.2%, $SD = 6.0$). They also revealed a significant interaction between this factor and Blocks, $F(3,114) = 4.03$, $p < .01$, showing a greater increase in accuracy for participants with several blocks (from 87.5% in block 1 to 91.9% in block 4) than for participants with one block (from 94.6% in block 1 to 95.1% in block 4). However, there was no significant interaction between Number of blocks and Type of list, $F(1,38) < 1$, ns , and no significant interaction between Number of blocks, Type of list, and Blocks, $F(3,114) = 2.00$, $p = .118$. Finally, linear trend tests indicated a significant increase in accuracy across blocks for the repeated list but not for the new lists. This was the case both for participants with one block ($F(1,23) = 14.07$, $p < .01$ for repeated; $F(1,23) = 2.29$, $p = .144$ for new) and for participants with several blocks ($F(1,15) = 15.060$, $p < .01$ for repeated; $F(1,15) = 2.97$, $p = .106$ for new).

2.3. Discussion

The results of Experiment 1 showed that tactile symbol recognition improved with training. However, performance improvement was restricted to those symbols that were repeated throughout the experiment, and did not occur for the new symbols that were introduced. The participants may thus have used stimulus-specific strategies of learning rather than extracting the perceptual rules that enable generalization of learning. In this experiment, the use of only four different tactile symbols in each block may have biased the participants toward adopting stimulus-specific strategies. For instance, it is possible to identify local (e.g., the presence of a curve for only one symbol in a list) or temporal (e.g., the duration of one symbol is shorter than the others) cues to recognize each symbol. With only four symbols the cost of maintaining such specific cues in short-term memory is not too important. However, the counterpart of such stimulus-specific strategies is that the cues specific to the learned symbols are no longer relevant when new symbols are introduced. As stimulus variability during learning facilitates generalization (Hussain et al., 2012), Experiment 2 therefore investigated whether learning a greater number of stimuli in each block encourages the participants to adopt generalized learning strategies.

Experiment 1 was also designed to evaluate whether tactile symbol recognition depends on the participants' natural preference for adopting self-centred or decentred perspectives. The results did not reveal any differences in recognition performance between the participants naturally adopting trunk-centred and those adopting decentred perspectives. This was true even when the variability in the emergence of the natural perspective was taken into account. Thus, both groups have similar results when participants were asked to recognize unambiguous symbols, contrary to the results of a previous study, in which decentred participants were better at recognizing ambiguous symbols (b, d, p, and q) from an unnatural perspective than self-centred participants (Arnold et al., 2016). The superiority of decentred observers in the recognition of ambiguous symbols may consequently be specific to assigning spatial coordinates (left, right, top, and bottom) to tactile stimulation and not to shape processing *per se*. This specificity is in line with the dissociation between processing object identity and processing object orientation, which has been suggested to rely on the ventral and dorsal visual streams respectively (Valyear, Culham, Sharif, Westwood, & Goodale, 2006).

3. Experiment 2

In Experiment 1, tactile symbol recognition only improved across blocks for repeated symbols but not for new symbols, revealing stimulus-specific rather than generalized learning. This second experiment investigated whether the learning strategy involved depends on the quantity of information to-be-learned and whether learning a greater number of symbols in each block favours a generalized learning. There were 6 symbols to learn in each list, with the same alternation of repeated and new symbols as in Experiment 1. If a more generalized learning is involved here, a symbol recognition improvement for both repeated and new symbols should be observed. As the recognition of unambiguous symbols did not depend on the participants' natural perspective in Experiment 1, and as naturally trunk-centred participants are more frequent than others (Arnold et al., 2016), only naturally trunk-centred participants were tested in this experiment. The symbols were always presented according to the participants' natural trunk-centred perspective.

3.1. Material and methods

3.1.1. Participants

Thirty-two participants (27 females and 5 males; mean age = 22.9 years, range = 18–40 years; eight participants were left-handed and 24 participants were right-handed) that all had a natural trunk-centred perspective completed the experiment. All the participants were naive to the purpose of the experiment. None had participated in the first experiment. Participants provided their informed consent and received payment for their participation. The experiment took approximately one hour to complete and was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (1991).

3.1.2. Apparatus

The apparatus was exactly the same as in Experiment 1.

3.1.3. Stimuli

The 20 symbols used in Experiment 1 and four additional symbols (the uppercase letters H, S, T, and U) were presented on the participant's stomach. The way the letters were traced was the same as in Experiment 1. The mean duration of symbols was 2188 ms ($SD = 586$). Four lists of six symbols were created with similar mean durations (List1: JKPZ36, 2142 ms; List2: FHLRT4, 2075 ms; List3: BCDQ25, 2392 ms; List4: EGNSU1, 2142 ms). Each of these lists was composed of four or five letters and one or two numbers.

3.1.4. Procedure

The procedure was similar to the one used in Experiment 1. In the first part of the experiment, in order to decrease the number of blocks necessary to identify their natural perspective, participants were explicitly instructed to adopt the easiest perspective for them rather than the most 'logical' perspective. To identify each participant's natural perspective, only one block was required for 25 participants, two blocks for two participants, and three blocks for five participants.

Once the participants' natural perspective was identified, they completed six blocks for the recognition task. One of the lists (repeated list; labelled A) was presented three times. The other three lists (new lists; labelled B through D) were presented once each. Therefore there were three blocks with the repeated list and three blocks with the new lists, which were alternated as follows: ABACAD for half of the participants and BACADA for the other half. Each of the four lists served as the repeated list for a fourth of the participants ($N = 8$). In addition, each list was presented the same number of times across participants as lists B, C, and D. Each block consisted of 60 trials (10 presentations of each symbol). At the beginning of each block, the participants were given six practice trials (one trial for each symbol) with a feedback

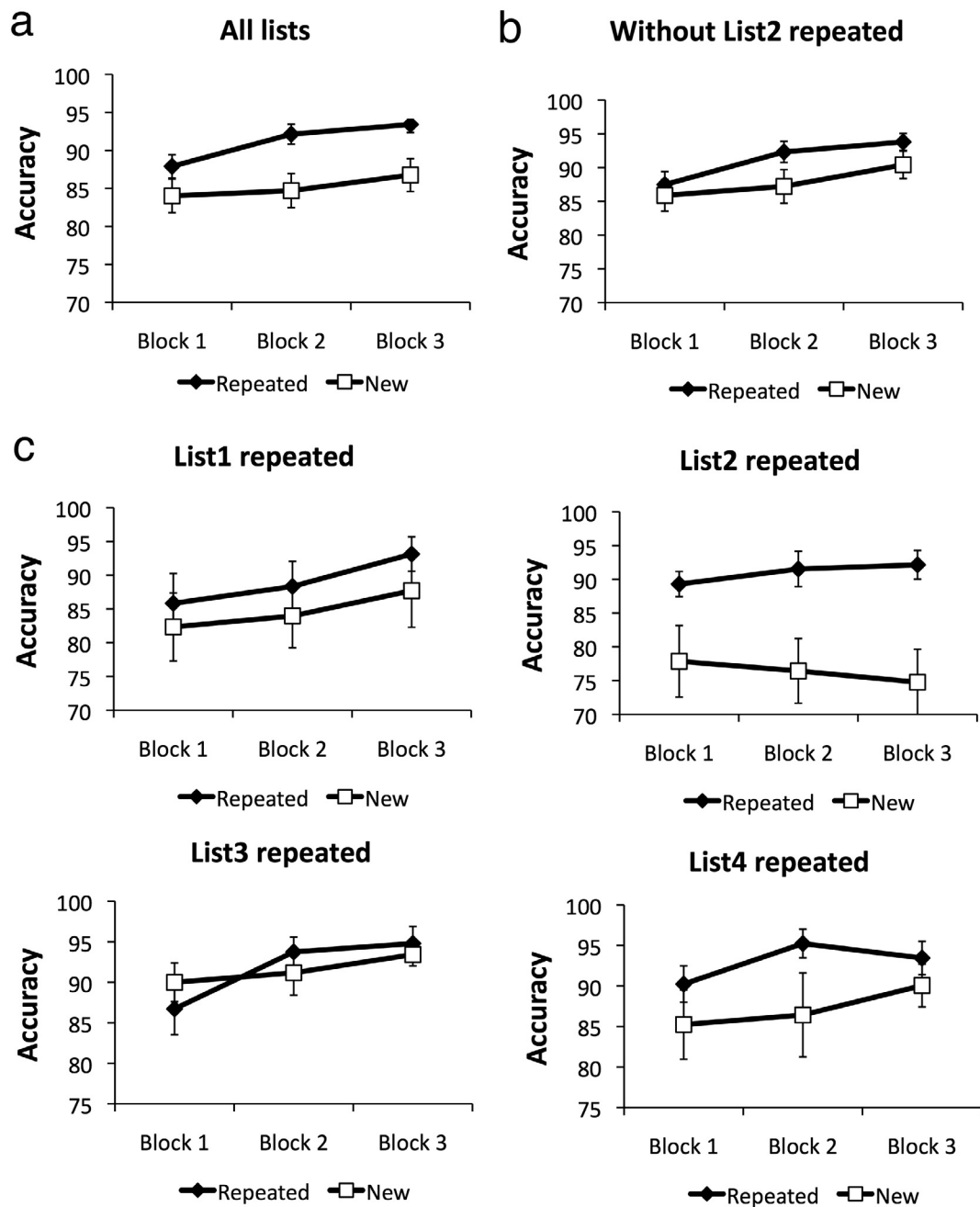


Fig. 3. Participants' accuracy during Experiment 2 as a function of Type of list (repeated, new) and Block. (a) When all the lists were included, accuracy increased across blocks for the repeated list only. (b) When excluding the participants who had List 2 as the repeated list, accuracy increased across blocks for both the repeated and new lists. (c) Details of the results for each list as the repeated list. Accuracy increased across blocks for the new lists except when List 2 was the repeated list. Error bars represent the standard errors of the means.

indicating the correct response at the end of each trial.

3.2. Results

Trials in which the participants failed to make a response before the trial was terminated (2.00% of trials) were not included in the data analyses. An ANOVA was conducted with Type of list (repeated, new) and Block (block 1, block 2, block 3) as within-participant factors. The results showed a significant effect of Block, $F(2,62) = 8.27, p < .001$, and, contrary to Experiment 1, no significant interaction between Block and Type of list, $F(2,62) = 1.51, p = .230$. This reveals a global increase in accuracy across blocks (block 1 = 86.5%, SD = 10.8; block 2 = 88.8%, SD = 11.0; block 3 = 90.5, SD = 10.1) (see Fig. 3a). The increase in accuracy was observed for both repeated (block 1 = 88.5%,

SD = 8.6; block 2 = 92.5%, SD = 7.5; block 3 = 93.7, SD = 6.0) and new lists (block 1 = 84.5%, SD = 12.5; block 2 = 85.0%, SD = 12.8; block 3 = 87.2, SD = 12.3). The linear trend test was however significant for the repeated list, $F(1,31) = 18.12, p < .001$, but not for the new lists, $F(1,31) = 1.97, p = .171$. There was also a significant effect of the Type of list, $F(1,31) = 20.40, p < .001$, with greater accuracy for repeated (91.5%, SD = 7.7) than for new lists (85.6%, SD = 12.4).

The absence of interaction between Type of List and Block suggests a global increase in accuracy across blocks but, nevertheless, there was no significant linear increase for the new lists. Thus, to try and account for the results of Experiment 2, the effect of each of the lists was investigated, to see whether the generalization of learning depends on the learned symbols. There was an increase in accuracy across blocks with the new lists when all the lists were repeated except for List 2 (see

Table 1
Number of horizontal, vertical, oblique, and curved features for the different lists in Experiment 1 and Experiment 2.

		Horizontal	Vertical	Oblique	Curve	Total	
Experiment 1	List 1 P Q Z 5	3	2	2	3	10	
	List 2 J K 3 6	2	2	2	4	10	
	List 3 F L R 4	4	5	1	1	11	
	List 4 B C D 2	1	2	1	5	9	
	List 5 E G N 1	4	4	3	1	12	
	Experiment 2	List 1 J K P Z 3 6	4	3	3	5	15
		List 2 F H L R T 4	6	8	1	1	16
		List 3 B C D Q 2 5	2	3	2	7	14
		List 4 E G N S U 1	4	4	3	4	15

Fig. 3c). The difference in accuracy between the repeated and the new lists was also the strongest when List 2 was repeated (13.4 points of percentage; 4.4, 0.2, and 5.8 points of percentage for the List 1, List 3, and List 4, respectively), showing strong specificity to the stimulus learned in this list. It is interesting to note that List 2 differed from the others by the variability in its letter features. Table 1 shows that the symbols composing List 2 were essentially made of vertical and horizontal features and that there were very few oblique and curved features. On the contrary, the different types of features were more equally distributed in List 1, List 3, and List 4. Thus, feature variability may also have played a role in the generalization of learning, with exposition to a small set of features (List 2) potentially limiting one's ability to recognize new symbols.

Accordingly, an ANOVA was conducted, this time without those participants who had List 2 as the repeated list. In this case, the interaction between Type of List and Block was not significant, $F(2,62) = 1.34$, $p = .271$, and the linear trend test was significant for both the repeated, $F(1,31) = 15.69$, $p < .001$, and the new lists, $F(1,31) = 5.93$, $p < .05$, showing a clear pattern of generalization (see Fig. 3b). Note that this was not the case when the participants who had the List 1, List 3, or List 4 as the repeated list were excluded from the analysis. In order to evaluate the role of feature variability in Experiment 1, the distribution of the different types of features in the different lists was also analysed. Table 1 shows that the different types of features were relatively well distributed in List 1, List 2, and List 5 whereas List 3 was essentially made of vertical and horizontal features and List 4 was essentially made of curved features. Thus an ANOVA was conducted with only the participants who had List 1, List 2, and List 5 as the repeated list. The results revealed a significant interaction between Type of List and Block, $F(3,69) = 5.98$, $p < .01$, and the linear trend test was significant only for the repeated list, $F(1,23) = 18.96$, $p < .001$, not for the new lists, $F(1,23) = 1.75$, $p = .199$, showing no pattern of generalization. In summary, the results of Experiment 2 indicate that participants implemented general learning strategies except when feature variability of the repeated list was relatively low. However, in Experiment 1, with a few learned symbols, stimulus-specific strategies were involved, independently of feature variability.

3.3. Discussion

Compared to the results of Experiment 1, the results of Experiment 2 are overall in favour of generalized learning strategies and they are compatible with the effect of stimulus variability on generalization (Hussain et al., 2012). When the number of symbols to learn is

increased (from four to six symbols in each list), stimulus-specific strategies may be too costly. For instance, it may be difficult to keep a specific spatio-temporal cue for each symbol to learn in working memory. As a consequence, participants try to extract general perceptual rules, which favour the subsequent recognition of unlearned stimuli. An alternative explanation would be that task difficulty influenced the degree of generalization. Indeed, the global recognition performance was significantly higher in Experiment 1 (mean accuracy = 93.5%, $SD = 4.8$; mean RT = 2420 ms, $SD = 360$), with four symbols to recognize in each block, than in Experiment 2 (mean accuracy = 88.6%, $SD = 8.4$; mean RT = 2743 ms, $SD = 287$), with six symbols, for both accuracy, $t(70) = 3.14$, $p < .01$ and RTs, $t(70) = 4.10$, $p < .001$. However, contrasting results have been reported for the effect of task difficulty, with some studies showing specificity for difficult tasks (Jeter et al., 2009; Wang et al., 2013) but other showing generalization (Liu & Weinsall, 2000).

The results of Experiment 2 also revealed that generalization depends on the symbols' feature variability. For one list of symbols among the four different lists, perceptual learning remained specific to the learned symbols. Compared to the other lists, this list consisted of symbols with a low variability, essentially made of vertical and horizontal strokes, with few oblique or curved features. However, the same analysis of feature variability conducted on the results of Experiment 1 did not show any influence of feature variability: stimulus-specific learning was observed for both homogeneous and heterogeneous lists of symbols. Overall, the results of Experiment 1 and Experiment 2 therefore show that generalization to new symbols depends both on the size of the stimulus set that is learned and on feature variability. When fewer symbols are learned, stimulus-specific strategies are involved, independently of feature variability. When the stimulus set is increased, generalized strategies are involved but feature variability is necessary to make these strategies efficient. This effect of variability during training is consistent with previous studies reporting greater generalization after learning objects from different exemplars (Baeck, Maes, Van Meel, & Op de Beeck, 2016).

Finally, one possibility is that the type of learned features also plays a role. It may be more difficult to generalize from horizontal and vertical to oblique and curved features than the other way round. This effect of symbol feature can be interpreted with the feature analysis theory of visual perception (Treisman & Gormican, 1988). According to this theory, basic visual features such as straight lines are coded in the visual brain as standards and other features such as oblique and curved lines are coded as a deviation from the standard. As a consequence, brain activation is more important when perceiving deviant than standard features. A possibility here is that tactile recognition of visual symbols involved similar low-level processes as in visual recognition and that learning heterogeneous symbols, made of horizontal, vertical, oblique, and curvature features, activated broader brain areas than learning homogeneous symbols. According to the RHT, this broader brain activation has subsequently facilitated learning generalization.

4. Experiment 3

Experiment 3 was designed to investigate generalization to changes in orientation. Tactile symbols were learned upright and then they had to be recognized rotated 90° to the left or to the right, or 180° (upside-down). In order to be able to directly compare the generalization to new stimuli and to new orientations, the same learning protocol as in Experiments 1 and 2 was used, with an alternation of repeated (upright) and new (rotated) orientations. If learning generalizes to changes in orientation, that is, if recognizing a learned symbol in a new orientation has no cost, an improvement in recognition performance for both the repeated and new orientations should be observed. On the contrary, if learning is specific to the learned orientation, an improvement in performance only for the repeated orientation should be observed instead. As in Experiment 2, only naturally trunk-centred participants

completed this experiment.

4.1. Material and methods

4.1.1. Participants

Twenty-four participants (16 females and 8 males; mean age = 23.1 years, range = 19–34 years; one participant was left-handed and 23 participants were right-handed) that all had a natural perspective centred on their trunk completed the experiment. All the participants were naive to the purpose of the experiment. None had participated in Experiment 1 or Experiment 2. Participants provided their informed consent and received payment for their participation. The experiment took approximately one hour to complete and was performed in accordance with the ethical standards laid down in the [Declaration of Helsinki \(1991\)](#).

4.1.2. Apparatus

The apparatus was the same as in Experiments 1 and 2.

4.1.3. Stimuli

The same four lists of six symbols as presented in Experiment 2 were used. For each symbol, one vibrotactile sequence was created for each orientation (upright, left-rotated, right-rotated, upside-down). The left-rotated orientation corresponded to a 90°-rotation of the symbol toward the participant's left-hand side. Therefore the top of the symbol was located on the left side of the trunk. In contrast, the right-rotated orientation corresponded to a 90°-rotation of the symbol toward the participant's right-hand side. Therefore the top of the symbol was located on the right side of the trunk. The upside-down condition corresponded to a 180°-rotation of the symbol, resulting in the top of the symbol being located on the bottom of the trunk.

4.1.4. Procedure

The procedure was similar to the one of Experiment 2. To identify each participant's natural perspective, only one block was required for 22 participants, two blocks for one participant, and three blocks for one participant.

After the identification of their natural perspective, the participants completed six blocks for the recognition task. For each participant, only one list was presented, with the same number of participants ($N = 6$) for each list. In each block, the symbols were presented with one out of the four orientations. The upright orientation (repeated, labelled A) was presented three times. The other three orientations (unrepeated, labelled B through D) were presented once each. Thus there were three blocks with the symbols presented upright and three blocks with the symbols rotated, that were alternated as follows: ABACAD for half of the participants and BACADA for the other half. Each rotated condition (90° left, 90° right, 180°) was presented the same number of times across participants as blocks B, C, and D. Each block consisted of 60 trials (10 presentations of each symbol). At the beginning of each block, the participants were given six practice trials (one trial for each symbol) with feedback indicating the correct response at the end of each trial.

4.2. Results

Trials in which the participants failed to make a response before the trial was terminated (0.26% of trials) were not included in the data analyses. An ANOVA was conducted with Type of orientation (repeated, new) and Block (block 1, block 2, block 3) as within-participant factors. The results showed a significant effect of Block, $F(2,46) = 9.67$, $p < .001$, and no significant interaction between Block and Type of orientation, $F(2,46) < 1$ (see [Fig. 4a](#)). The increase in accuracy was observed for both repeated (block 1 = 84.4%, $SD = 13.4$; block 2 = 88.2%, $SD = 13.2$; block 3 = 90.4%, $SD = 10.7$) and new (block 1 = 77.9%, $SD = 16.5$; block 2 = 81.8%, $SD = 14.6$; block 3 = 82.8%, $SD = 16.1$) orientations. The linear trend test was

significant for both the repeated orientation, $F(1,23) = 12.48$, $p < .01$, and the new orientations, $F(1,23) = 5.88$, $p < .05$. There was also a significant effect of Type of orientation, $F(1,23) = 25.65$, $p < .001$, with greater accuracy for repeated (87.7%, $SD = 12.6$) than for new orientations (80.8%, $SD = 15.7$).

In order to investigate a possible effect of the symbols' orientation on learning generalization, the accuracy was also computed as a function of the angle of rotation (90° left, 90° right, and 180°) from the upright orientation (see [Fig. 4b](#)). The results first revealed that global accuracy was similar for the three angles of rotation (81.3%, $SD = 16.5$, for the 90° left; 81.3%, $SD = 15.0$, for the 90° right; 80.0%, $SD = 16.2$, for the 180°). It should be underlined that this experiment was designed to investigate the participants' ability to recognize learned symbols with a new orientation in each session. As a consequence, the evaluation of performance improvement across blocks as a function of each symbol's orientation is based on between-participant comparisons with a small sample size ($n = 6$) and can be only descriptive. [Fig. 4b](#) illustrates that recognition performance improved across blocks for all the symbols' orientations except for the 90°-left orientation for which performance increased in the second block and then decreased in the third block.

4.3. Discussion

The results of Experiment 3 revealed generalization to previously learned symbols presented in a new orientation and they are compatible with previously reported results on generalization to new orientations. Even though perceptual learning is often highly specific to orientation (e.g., [Hussain, Sekuler, & Bennett, 2009](#)), generalization to new orientations has been reported to be easier than generalization to new set of stimuli ([Baeck, Windey, & Op de Beeck, 2012](#)). The sequential presentation of the tactile symbols in our study may have also facilitated generalization to orientation. Indeed, the spatio-temporal characteristics of each symbol may easily be recognized independently of the way the symbol is oriented on the body surface. For instance, the sequence of one long stroke followed by two short strokes for the letter K is easily perceived in each orientation. That is to say, the static presentation of a symbol might be seen to facilitate generalization to the same extent.

The results of Experiment 3 are also compatible with previous studies on visual recognition of rotated letters and digits, which showed that recognition depends on angular rotation as a function of the task. When the task consists in deciding whether the symbol is normal or mirror-reversed, there is an effect of angular rotation on recognition performance ([Cooper & Shepard, 1973](#)). On the contrary, when the task consists in identifying the alphanumeric symbol, there is no effect of angular rotation on recognition performance, showing that alphanumeric symbols are recognized through the extraction of critical features invariant to the symbol's orientation ([Corballis, Zbrodoff, Shetzer, & Butler, 1978](#); [Eley, 1982](#)). In the present study, the absence of difference in global accuracy between the different angles of rotation from the upright orientation may be explained by the use of an identification task rather than a verification task.

Regarding the rotation of the symbols on the stomach, it is interesting to note that symbol recognition may have been facilitated for the 180°-rotated orientation because recognizing a 180°-rotated symbol presented on the stomach with a trunk-centred perspective is close to adopting a head-centred perspective. Indeed, adopting a head-centred perspective results in perceiving the symbol upright but mirror-reversed (except for the symmetrical symbols). As the task was not to decide whether the symbol was normal or mirror-reversed, and as there was no pair of symmetrical symbols in the lists of symbols presented to the participants, adopting a head-centred perspective may have been an easier perceptual strategy than trying to recognize rotated symbols.

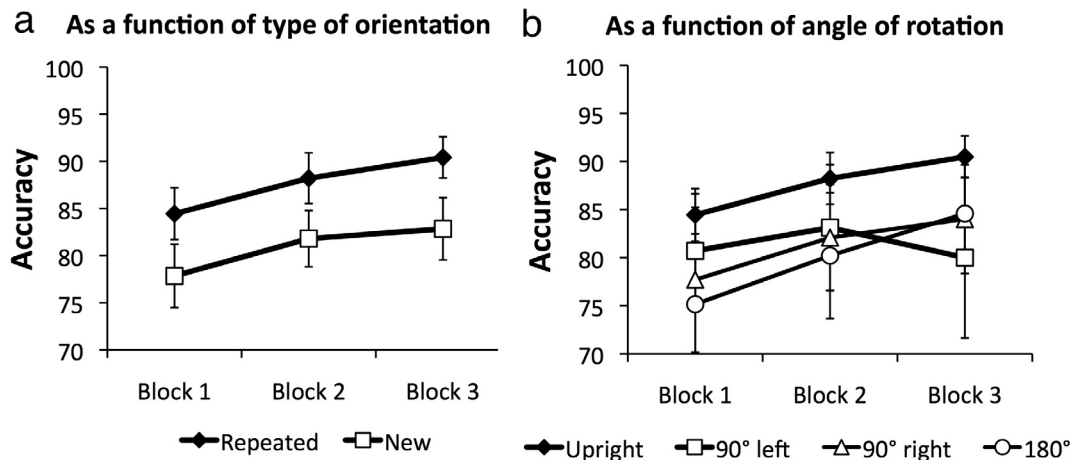


Fig. 4. Participants' accuracy in Experiment 3 as a function of (a) Type of orientation (repeated, new) and Block and (b) Angle of rotation and Block. Error bars represent the standard errors of the means.

5. General discussion

The present study investigated whether learning to recognize the tactile conversion of visual symbols generalizes to new stimuli and new orientations. The results show that the generalization to new stimuli depends both on the size of the stimulus set and on feature variability. Stimulus-specific learning strategies are involved when learning a limited number of stimuli whereas generalized strategies are involved when increasing the number of learned stimuli. However, in the latter case, feature variability is necessary to achieve generalization. When the learned symbols are homogeneous and composed essentially of vertical and horizontal strokes, learning does not generalize to new symbols. Our results also reveal that tactile perceptual learning generalizes to new orientations.

The present study reveals that generalization of learning depends on both the quantity and diversity of information presented during learning. Nonetheless further studies would be necessary to identify the specific factors that facilitate generalization. The most likely hypothesis is that increasing the set of learned stimuli prevents observers from involving stimulus-specific learning strategies. As a consequence, observers are forced to identify the general perceptual rules that can be applied to new stimuli. The better generalization performance reached in Experiment 2 than in Experiment 1 can also result from a difference in task difficulty. Note that if this were to be the case, this would go against the RHT of perceptual learning (Ahissar & Hochstein, 2004), which posits generalization for easy tasks and specificity for difficult tasks. In our experiments, the use of short blocks of trials and the alternation of learned and new symbols might also have contributed to generalization by preventing sensory adaptation. However, such use of short blocks and alternation were not sufficient to induce generalization in Experiment 1. Therefore it is unlikely that these characteristics of the learning protocol were solely responsible for the generalization of learning observed in Experiment 2.

The generalization to new tactile stimuli found in our study and the generalization that has been previously reported when using visual-to-auditory conversion devices (Brown & Proulx, 2013; Kim & Zatorre, 2008) can be interpreted in the light of the multisensory RHT proposed by Proulx et al. (2014). According to the classic RHT, generalization of learning benefits from broad brain activations during learning. According to the multisensory RHT, multisensory tasks produce broader brain activation than unisensory tasks in two possible ways. Cross-modal interactions might occur through direct connections between low-level unisensory areas (i.e., visual, auditory, and tactile primary cortex) or through higher-level multisensory areas where the objects are represented independently of the input sensory modality. Therefore, in the case of using a visual-to-tactile or visual-to-auditory substitution

device, direct connections can occur between tactile and visual, or between auditory and visual primary cortices. The other possibility is that the processing of tactile or auditory stimuli first progresses from tactile or auditory primary cortices to high-level object processing areas such as the lateral occipital complex (Amedi et al., 2007) and then cascade down back to visual areas. According to these two possibilities, the multisensory nature of the task produces broad brain activation and may facilitate the generalization to new stimuli.

A question remaining open is whether generalization was indeed facilitated by the multisensory nature of the task, as it corresponds to tactile recognition of visual symbols or, instead, if generalization to new stimuli is a characteristic of tactile perceptual learning itself. This is a difficult alternative to solve given that the generalization to new sets of stimuli in tactile perceptual learning has been the subject of comparatively less investigation than in visual perceptual learning. In one previous study, learning to recognize tactile patterns was found to transfer to new stimuli (Epstein, Hugues, Schneider, & Bach-y-Rita, 1989). However, the task at hand consisted in matching the tactile patterns with their visual analogue. In this case, a similar multisensory processing cannot be excluded either. In further studies, using a direct comparison of a purely tactile task with a visuo-tactile task will allow to evaluate the specific role of multisensory processing in tactile perceptual learning.

Regarding generalization to new orientations, the results obtained in our study are compatible with previous results on visual recognition of rotated alphanumeric symbols (Corballis et al., 1978; Eley, 1982), showing that alphanumeric symbols are learned through the extraction of critical features invariant to the symbol's orientation. The sequential presentation of symbols may also have reinforced orientation-invariant recognition, as spatiotemporal features rather than purely spatial ones are more likely to have been extracted here. However, the hypothesis that people are able to recognize previously learned symbols independently of their orientation seems incompatible with the influence of expertise on orientation effects. In vision, it is well known that inverting faces (i.e., 180°-rotation) dramatically decreases face recognition (Yin, 1969). This inversion effect is partly explained by the strong habit to perceive faces upright rather than rotated. An inversion effect has also been reported for unnatural objects (e.g., Greebles) that have received expertise (Gauthier, Williams, Tarr, & Tanaka, 1998). As faces, alphanumeric symbols are more frequently perceived upright than rotated. Moreover, in the tactile sensory modality, Behrmann and Ewell (2003) have shown that becoming an expert in tactile recognition induces an inversion effect. It is thus surprising that such inversion effects were not observed for the tactile recognition of visual symbols. One possibility for this discrepancy is that the duration of the present study was insufficient for participants to consolidate learning

equivalent to expertise. Another possibility is that the alternation of blocks with upright and rotated orientations, rather than a complete learning phase with upright symbols followed by test blocks with rotated symbols, prevents the facilitation effect for the upright condition. The fact that alphanumerical symbols are less complex items than faces may also have limited the involvement of specific processes such as configural processing (i.e., processing not only features, but also the relations among features), which is often characteristic of expertise (Gauthier & Tarr, 2002).

Finally, the orientation-independent perceptual learning found in our study may reflect a distal attribution process, which is an important characteristic of sensory substitution. Distal attribution corresponds to the fact that, after training to use a visual-to-tactile device, the tactile stimulation felt on the skin becomes directly attributed to external objects, as it is the case for vision. Thus distal attribution is often considered as a criterion of the involvement of visual-like processes when using a sensory substitution device. One claim made by Bach-y-Rita was that, as a consequence of distal attribution, the tactile matrix of a visual-to-tactile device can be moved from one body surface to another without loss of perceptual abilities in trained users (Bach-y-Rita & Kerckel, 2003). This claim has been confirmed by a study reporting a transfer of learning from trained to untrained body surfaces in a tactile recognition task of visual symbols (Arnold & Auvray, 2014). Distal attribution processes may also contribute here to tactile recognition of visual stimuli independently of the orientation of the tactile stimulation on the body surface.

To conclude, the present study provides new insights into the understanding of tactile perceptual learning and brain plasticity. Tactile perceptual learning appears to share some characteristics with visual perceptual learning (influence of stimulus variability and task difficulty, representation of standard features similar to visual features). This similarity may reflect the involvement of supramodal areas in both visual and tactile object recognition (Kupers & Ptito, 2011; Pascual-Leone & Hamilton, 2001). Regarding sensory substitution, the similarity in processes is compatible with the view that perception with a sensory substitution device is vertically integrated, retaining characteristics of the substituted (e.g., vision) and the substituting (e.g., audition or touch) sensory modalities (Arnold, Pesnot-Lerousseau, & Auvray, in press; Deroy & Auvray, 2012; Deroy & Auvray, 2014). There are also applied implications, in particular for the design of learning protocols for sensory substitution, suggesting that short learning sessions with high variability and diversity will facilitate generalization and will allow for a more optimal use of the device in real-life conditions. However, one remaining question is how to achieve complete generalization, that is, how to rapidly gain optimal level of performance for entirely new objects. One of the possible cues is obviously the amount of learning. Daily use of the device would allow users to become experts. Learning would also benefit from a highly diversified use of the device, with perception of different categories of complex objects and of different exemplars of the same category. Finally, an active exploration of the external world with the device, rather than a passive reception of stimuli, would also reinforce perceptual learning via the emergence of sensorimotor contingencies.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.visres.2017.11.007>.

References

- Ahissar, M., & Hochstein, S. (2004). The reverse hierarchy theory of visual perceptual learning. *Trends in Cognitive Science*, 8, 457–464.
- Amedi, A., Stern, W. M., Camprodon, J. A., Bermpohl, F., Merabet, L., Rotman, S., & Pascual-Leone, A. (2007). Shape conveyed by visual-to-auditory sensory substitution activates the lateral occipital complex. *Nature Neuroscience*, 10, 687–689.
- Arno, P., Vanlierde, A., Streel, E., Wanet Defalque, M. C., Sanabria-Bohorquez, S., & Veraart, C. (2001). Auditory substitution of vision: pattern recognition by the blind. *Applied Cognitive Psychology*, 15, 509–519.
- Arnold, G., Pesnot-Lerousseau, J., & Auvray, M. (in press). Individual differences in sensory substitution. *Multisensory Research*.
- Arnold, G., & Auvray, M. (2014). Perceptual learning: Tactile letter recognition transfers across body surfaces. *Multisensory Research*, 27, 71–90.
- Arnold, G., Spence, C., & Auvray, M. (in press). A unity of the self or a multiplicity of locations? How the graphesthesia task sheds light on the role of spatial perspectives in bodily self-consciousness. *Consciousness & Cognition*.
- Arnold, G., & Siéhoff, E. (2012). Timing constraints of temporal view association in face recognition. *Vision Research*, 54, 61–67.
- Arnold, G., Spence, C., & Auvray, M. (2016). Taking someone else's spatial perspective: Natural stance or effortful decentring? *Cognition*, 148, 27–33.
- Auvray, M. (2004). *Immersion et perception spatiale: l'exemple des dispositifs de substitution sensorielle* [Immersion and spatial perception: the example of sensory substitution devices] (Unpublished doctoral dissertation). EHESS, Paris, France.
- Auvray, M., Hannonet, S., & O'Regan, J. K. (2007). Learning to perceive with a visuo-auditory substitution system: Localization and object recognition with The Voice. *Perception*, 36, 416–430.
- Auvray, M., & Myin, E. (2009). Perception with compensatory devices: From sensory substitution to sensorimotor extension. *Cognitive Science*, 33, 1036–1058.
- Bach-y-Rita, P., & Kerckel, S. W. (2003). Sensory substitution and the human-machine interface. *Trends in Cognitive Sciences*, 7, 541–546.
- Baek, A., Maes, K., Van Meel, C., & Op de Beeck, H. P. (2016). The transfer of object learning after training with multiple exemplars. *Frontiers in Psychology*, 7, 1386.
- Baek, A., Windey, L., & Op de Beeck, H. P. (2012). The transfer of object learning across exemplars and their orientation is related to perceptual similarity. *Vision Research*, 68, 40–47.
- Behrmann, M., & Ewell, C. (2003). Expertise in tactile pattern recognition. *Psychological Science*, 14, 480–492.
- Brown, D. J., & Proulx, M. J. (2013). Increased signal complexity improves the breadth of generalization in auditory perceptual learning. *Neural Plasticity*, 2013, 879047.
- Cooper, L. A., & Shepard, R. N. (1973). Chronometric studies of the rotation of mental images. In W. G. Chase (Ed.), *Visual information processing* (pp. 75–176). New York: Academic Press.
- Corballis, M. C., Zbrodoff, N. J., Shetzer, L. I., & Butler, P. B. (1978). Decisions about identity and orientation of rotated letters and digits. *Memory and Cognition*, 6, 98–107.
- Deroy, O., & Auvray, M. (2012). Reading the world through the skin and ears: a new perspective on sensory substitution. *Frontiers in Psychology*, 3, 457.
- Deroy, O., & Auvray, M. (2014). A crossmodal perspective on sensory substitution. In S. Biggs, M. Matthen, & D. Stokes (Eds.), *Perception and its modalities* (pp. 327–349). Oxford: Oxford University Press.
- Dutilh, G., Krypotos, A. M., & Wagenmakers, E. J. (2011). Task-related versus stimulus-specific practice: A diffusion model account. *Experimental Psychology*, 58, 434–442.
- Eley, M. G. (1982). Identifying rotated letter-like symbols. *Memory and Cognition*, 10, 25–32.
- Epstein, W., Hughes, B., Schneider, S. L., & Bach-y-Rita, P. (1989). Perceptual learning of spatiotemporal events: Evidence from an unfamiliar modality. *Journal of Experimental Psychology: Human Perception and Performance*, 15, 28–44.
- Fahle, M. (2005). Perceptual learning: Specificity versus generalization. *Current Opinion in Neurobiology*, 15, 154–160.
- Fahle, M. E., & Poggio, T. E. (2002). *Perceptual learning*. Cambridge, MA, USA: MIT Press.
- Furmanski, C. S., & Engel, S. A. (2000). Perceptual learning in object recognition: Object specificity and size invariance. *Vision Research*, 40, 473–484.
- Gauthier, I., & Tarr, M. J. (2002). Unraveling mechanisms for expert object recognition: Bridging brain activity and behavior. *Journal of Experimental Psychology: Human Perception and Performance*, 28, 431–446.
- Gauthier, I., Williams, P., Tarr, M. J., & Tanaka, J. (1998). Training “Greeble” experts: A framework for studying expert object recognition processes. *Vision Research*, 38, 2401–2428.
- Haggard, P., Taylor-Clarke, M., & Kennett, S. (2003). Tactile perception, cortical representation and the bodily self. *Current Biology*, 13, R170–R173.
- Harrar, V., Spence, C., & Makin, T. R. (2014). Topographic generalization of tactile perceptual learning. *Journal of Experimental Psychology: Human Perception and Performance*, 40, 15–23.
- Harris, H., Gliksberg, M., & Sagi, D. (2012). Generalized perceptual learning in the absence of sensory adaptation. *Current Biology*, 22, 1813–1817.
- Hartcher-O'Brien, J., & Auvray, M. (2014). The process of distal attribution illuminated through studies of sensory substitution. *Multisensory Research*, 27, 421–441.
- Hussain, Z., Bennett, P. J., & Sekuler, A. B. (2012). Versatile perceptual learning of

- textures after variable exposures. *Vision Research*, 61, 89–94.
- Hussain, Z., Sekuler, A. B., & Bennett, P. J. (2009). Perceptual learning modifies inversion effects for faces and textures. *Vision Research*, 49, 2273–2284.
- Jeter, P. E., Doshier, B. A., Liu, S. H., & Lu, Z. L. (2010). Specificity of perceptual learning increases with increased training. *Vision Research*, 50, 1928–1940.
- Jeter, P. E., Doshier, B. A., Petrov, A., & Lu, Z. L. (2009). Task precision at transfer determines specificity of perceptual learning. *Journal of Vision*, 9, 1–13.
- Kaczmarek, K. A., & Haase, S. J. (2003). Pattern identification and perceived stimulus quality as a function of stimulation waveform on a fingertip-scanned electrotactile display. *IEEE Transactions on Neural Systems and Rehabilitation Engineering*, 11, 9–16.
- Kim, J. K., & Zatorre, R. J. (2008). Generalized learning of visual-to-auditory substitution in sighted individuals. *Brain Research*, 1242, 263–275.
- Kim, J. K., & Zatorre, R. J. (2010). Can you hear shapes you touch? *Experimental Brain Research*, 202, 747–754.
- Kupers, R., & Ptito, M. (2011). Insights from darkness: What the study of blindness has taught us about brain structure and function. *Progress in Brain Research*, 192, 17–31.
- Levy-Tzedek, S., Hanassy, S., Abboud, S., Maidenbaum, S., & Amedi, A. (2012). Fast, accurate reaching movements with a visual-to-auditory sensory substitution device. *Restorative Neurology and Neuroscience*, 30, 313–323.
- Levy-Tzedek, S., Novick, I., Arbel, R., Abboud, S., Maidenbaum, S., Vaadia, E., & Amedi, A. (2012). Cross-sensory transfer of sensory-motor information: visuomotor learning affects performance on an audiomotor task, using sensory-substitution. *Scientific Reports*, 2, 949.
- Liu, Z., & Weinshall, D. (2000). Mechanisms of generalization in perceptual learning. *Vision Research*, 40, 97–109.
- Nagarajan, S. S., Blake, D. T., Wright, B. A., Byl, N., & Merzenich, M. M. (1998). Practice-related improvements in somatosensory interval discrimination are temporally specific but generalize across skin location, hemisphere, and modality. *Journal of Neuroscience*, 18, 1559–1570.
- Newell, F. N., Ernst, M. O., Tjan, B. S., & Bühlhoff, H. H. (2001). Viewpoint dependence in visual and haptic object recognition. *Psychological Science*, 12, 37–42.
- Pascual-Leone, A., & Hamilton, R. (2001). The metamodal organization of the brain. *Progress in Brain Research*, 134, 427–445.
- Pollok, B., Schnitzler, I., Mierdorf, T., Stoerig, P., & Schnitzler, A. (2005). Image-to-sound conversion: Experience-induced plasticity in auditory cortex of blindfolded adults. *Experimental Brain Research*, 167, 287–291.
- Proulx, M. J., Brown, D. J., Pasqualotto, A., & Meijer, P. (2014). Multisensory perceptual learning and sensory substitution. *Neuroscience & Biobehavioral Reviews*, 41, 16–25.
- Renier, L., Collignon, O., Poirier, C., Tranduy, D., Vanlierde, A., Bol, A., ... De Volder, A. G. (2005). Cross-modal activation of visual cortex during depth perception using auditory substitution of vision. *NeuroImage*, 26, 573–580.
- Sampaio, E., Maris, S., & Bach-y-Rita, P. (2001). Brain plasticity: 'Visual' acuity of blind persons via the tongue. *Brain Research*, 908, 204–207.
- Sathian, K., & Zangaladze, A. (1997). Tactile learning is task specific but transfers between fingers. *Perception and Psychophysics*, 59, 119–128.
- Sigman, M., & Gilbert, C. D. (2000). Learning to find a shape. *Nature Neuroscience*, 3, 264–269.
- Striem-Amit, E., Guendelman, M., & Amedi, A. (2012). 'Visual' acuity of the congenitally blind using visual-to-auditory sensory substitution. *PLoS ONE*, 7, e33136.
- Treisman, A., & Gormican, S. (1988). Feature analysis in early vision: Evidence from search asymmetries. *Psychological Review*, 95, 15–48.
- Valyear, K. F., Culham, J. C., Sharif, N., Westwood, D., & Goodale, M. A. (2006). A double dissociation between sensitivity to changes in object identity and object orientation in the ventral and dorsal visual streams: a human fMRI study. *Neuropsychologia*, 44, 218–228.
- Wang, X., Zhou, Y., & Liu, Z. (2013). Transfer in motion perceptual learning depends on the difficulty of the training task. *Journal of Vision*, 13, 1–9.
- World Medical Association (1991). Declaration of Helsinki. *Law, Medicine & Health Care: A Publication of the American Society of Law & Medicine*, 19, 264–265.
- Yanagida, Y., Kakita, M., Lindeman, R. W., Kume, Y., & Tetsutani, N. (2004). Vibrotactile letter reading using a low-resolution tactor array. *Proceedings of the 12th Symposium on Haptic Interfaces for Virtual Environment and Teleoperator Systems*, 400–406.
- Yi, D. J., Olson, I. R., & Chun, M. M. (2006). Shape-specific perceptual learning in a figure-ground segregation task. *Vision Research*, 46, 914–924.
- Yin, R. K. (1969). Looking at upside-down faces. *Journal of Experimental Psychology*, 81, 141–145.