Card posting does not rely on visual orientation:
A challenge to past neuropsychological dissociations

Constanze Hesse[1*], Kamilla Bonnesen[1], Volker Franz[2] & Thomas Schenk[3]

21/06/2021

Key words: oblique effect, action, perception, task demands, two-visual streams, biomechanical constraints

*Correspondence should be addressed to:

Dr. Constanze Hesse
School of Psychology
University of Aberdeen
King's Campus
AB24 3FX
United Kingdom
e-mail: c.hesse@abdn.ac.uk
phone: +44 (0)1224 273215

---

[1] School of Psychology, University of Aberdeen, Aberdeen, UK
[2] Department of Neuropsychology, Ludwig-Maximilians University, Munich, Germany
[3] Experimental Cognitive Science, Eberhard Karls University, Tuebingen, Germany

<u>Abstract</u>

A common set of tasks frequently employed in the neuropsychological assessment of patients with visuomotor or perceptual deficits are the card-posting and the perceptual orientation matching tasks. In the posting task, patients have to post a card (or their hand) through a slot of varying orientations while the matching task requires them to indicate the slot's orientation as accurately as possible. Observations that damage to different areas of the brain (dorsal vs. ventral stream) is associated with selective impairment in one of the tasks - but not the other - has led to the suggestion that different cortical pathways process visual orientation information for perception versus action. In three experiments, we show that this conclusion may be premature as posting does not seem to rely on the processing of visual orientation information but is instead performed using obstacle avoidance strategies that require an accurate judgement of egocentric distances between the card's and the slot's edges. Specifically, we found that while matching is susceptible to the oblique effect (i.e., common perceptual orientation bias with higher accuracy for cardinal than oblique orientations), this was not the case for posting, neither in immediate nor in memory-guided conditions. In contrast to matching, posting errors primarily depended on biomechanical demands and reflected a preference for performing efficient and comfortable movements. Thus, we suggest that previous dissociations between perceptual and visuomotor performance in letter posting tasks are better explained by impairments in egocentric and allocentric spatial processing than by independent visual processing systems.

Introduction

Neuropsychological studies generally aim to understand the relationship between brain functions and (human or animal) behaviour. To reach valid conclusions about this relationship, investigations rely on reliable, and often standardised, neuropsychological testing methods used for both the study of neurological patients as well as neurologically healthy humans (clinical vs. experimental neuropsychology). Yet, the more complex the behaviour of interest is, the more difficult it becomes to find experimental/behavioural tasks that reliably and unambiguously uncover specific features of the nervous system. For example, while standardised tests to assess visual and perceptual functions in humans have been available for up to over a century (visual acuity: Snellen chart (Snellen, 1862), colour vision: Ishihara Test (Ishihara, 1917), stereovision: random dot stereogram (Julesz, 1971)), tests assessing the visual guidance of action have a comparatively short history and tend to be much less standardised. This may partly be owed to the fact that the systematic investigation and description of human movement patterns relied on technological advances and only really started with the wider availability of video-based recording systems (Jeannerod, Long, & Baddeley, 1981).

An example for a commonly used task to assess visual guidance of movements in neuropsychological patients is the hand-orientation or letter-posting task where patients are asked to move their hand (or a card) through a slot of varying orientations. Early versions of this task were used to investigate the cortical control of visually-guided hand movements in non-human primates (Haaxma & Kuypers, 1974; Haaxma & Kuypers, 1975). Subsequently, Perenin and Vighetto (1988) adapted this task to investigate and quantify the visuomotor deficits in patients suffering from optic ataxia. Using this task, Perenin and Vighetto showed that optic ataxia patients exhibit specific impairments in the visual guidance of arm movements while their perceptual functions remained relatively intact.

A few years later, the task was employed and adapted to assess the pattern of impaired and retained functions in patient DF – a now-famous neuropsychological case who suffered from visual form agnosia caused by bilateral damage to the cortical ventral stream areas (Goodale, Milner, Jakobson, & Carey, 1991; Milner et al., 1991). Employing the posting-task (requiring the patient to either post her hand or a card through a slot of varying orientations), it was established that she had no trouble with the visuomotor guidance of arm and hand movements despite a clear deficit in several tests that assessed her perceptual orientation discrimination abilities. These perceptual tests required the patient to verbally report orientations or to make perceptual matches by either turning a rotatable disk or a hand-held card to match the

orientation of the posting slot. Patient DF's profound difficulties in using visual orientation information in perceptual tasks despite having no problem using *the same* information to perform visually guided actions were interpreted as demonstrating a classical dissociation between perceptual and visuomotor processes (Goodale & Milner, 1992; Goodale et al., 1991). In combination with the earlier reports from optic ataxia patients who seem to show the exact opposite pattern of behaviour (Perenin & Vighetto, 1988), it was suggested that the two disorders (i.e., optic ataxia and visual form agnosia) form a double-dissociation (Goodale & Milner, 2004; Milner & Goodale, 1995). As the cortical lesions of optic ataxia patients are primarily found in areas of the dorsal cortical stream (Jeannerod, 1988; Milner, Dijkerman, McIntosh, Rossetti, & Pisella, 2003; Perenin & Vighetto, 1988) and lesions of visual form agnosic patient DF are focused on ventral stream areas (James, Culham, Humphrey, Milner, & Goodale, 2003; Milner et al., 1991), this double-dissociation has been put forward as strong evidence for the idea that there are two functionally segregated systems: the dorsal system that mediates vision for action and the ventral system that mediates vision for perception – also known as the perception-action model (Milner & Goodale, 1995, 2006).

However, it is important to point out that the argument that there is a dissociation in performance between perceptual and visuomotor tasks relies on the assumption that both tasks test the same visual attribute. In the case of orientation matching versus posting this implies that posting also requires participants to explicitly process visual orientation information (Goodale & Milner, 2004; Goodale et al., 1991; Perenin & Vighetto, 1988).

In a previous article (Hesse, Franz, & Schenk, 2011), we argued that this might not be a valid assumption to make as posting could potentially also be solved as an obstacle avoidance task. This idea is based on the finding that the successful avoidance of collisions is one of the major factors that drive the planning of human hand movements (Lommertzen, E Silva, Cuijpers, & Meulenbroek, 2009; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 1999). Applied to posting this means that if participants guide the movement of their hand or card such that they ensure the edges clear the edges of the posting slot, they will automatically adopt an orientation that closely reflects the slot's orientation - but without the need to process orientation information explicitly. We provided evidence for this idea by showing that if we use a wider slot and a card which is only slightly smaller than the slot itself, about half the participants adopt the strategy of posting the card diagonally (rather than aligned with the slot's orientation). As diagonal posting allowed a larger clearance of the slot edges, we argued that these participants perform posting using an obstacle-avoidance strategy.

Yet, this argument may not be compelling enough for everyone, as one could argue that posting in this case may have still been based on orientation perception, only that now a different orientation was used (i.e. orientation of the slot's diagonal rather than its longest side, also see Figure 1 in Hesse et al., 2011). Here, we suggest and test a new, more robust, approach to determine whether or not posting relies on visual orientation perception. Our approach is based on the observation that humans tend to show clear biases in orientation perception (Appelle & Gravetter, 1985; Campbell, Kulikowski, & Levinson, 1966; Mikellidou, Cicchini, Thompson, & Burr, 2015; Vogels & Orban, 1985). The finding that we tend to be more accurate to produce, detect, and/or discriminate cardinal orientations (i.e., vertical and horizontal) as compared to oblique ones has been coined the *oblique effect* – and has been reliably observed in both perceptual tasks as well as in haptic matching tasks (e.g., Campbell et al., 1966; Corwin, Moskowitz-Cook, & Green, 1977; Cuijpers, Kappers, & Koenderink, 2000; Hermens & Gielen, 2003; Kappers & Koenderink, 1999; Lechelt & Verenka, 1980; Mikellidou et al., 2015; Soechting & Flanders, 1993). Consequently, one would expect that if orientation perception underlies posting, an oblique effect should also be apparent in this task. In contrast, we would predict that if posting does not require visual orientation processing but relies on different visual cues (e.g., the slot's edges) and strategies (such as obstacle avoidance), no oblique effect would occur.

To our knowledge, only one study has looked at the accuracy of posting and matching performance for cardinal and oblique slot orientations and found an oblique effect for (passive) perceptual matching but not for visuomotor posting (Gosselin-Kessiby, Messier, & Kalaska, 2008). Even-though the finding that posting is immune to the oblique effect is in-line with our prediction, there is an important caveat: the perception-action model may make the same prediction. Specifically, the finding that certain perceptual biases and errors are found only in perceptual tasks but not in corresponding action tasks has traditionally been interpreted as support that vision for action and vision for perception are dissociated (e.g., Aglioti, DeSouza, & Goodale, 1995; Ganel, Chajut, & Algom, 2008; Ganel & Goodale, 2003; Haffenden & Goodale, 1998). Thus, if we found a dissociation between matching and posting with respect to the oblique effect we had two potential explanations/hypotheses that might account for this: The first hypothesis is that posting relies on different strategies than matching and uses different sensory information. Specifically, it is assumed that matching, but not posting, relies on visual orientation information. We will call this the *strategy hypothesis*. The second hypothesis, which is associated with the perception-action model, argues that both tasks,

posting and matching, use the same visual information but process it differently. In perceptual tasks, visual information is processed in the ventral stream and is subject to perceptual biases such as the oblique effect. In contrast, when performing action tasks, visual information is processed in the dorsal stream that is immune to perceptual biases, including the oblique effect. We will call this second hypothesis, the *processing hypothesis.* The *processing hypothesis* assumes that visual orientation is represented in a different format and processed in a different visual stream depending on whether a perceptual or visuomotor task is performed.

As pointed out above, the issue is that both the *strategy* and the *processing hypothesis* predict that matching - but not posting - is subject to the oblique effect. So, how can we solve the ambiguity between the two different hypotheses?

Help comes from another assumption of the perception-action model. According to the perception-action model, metrically correct and unbiased visuomotor representations of the dorsal stream are only available when visual information is present during movement planning. Consequently, if a delay is introduced between seeing the target and initiating the movement, it is assumed that actions have to rely on the stored perceptual representations of the ventral stream (e.g., Goodale, Kroliczak, & Westwood, 2005; Goodale, Westwood, & Milner, 2004; Milner et al., 2003; Westwood & Goodale, 2003). Consistent with this assumption it has been found that perceptual biases that affect perception but not immediate actions become apparent when actions are delayed and have to be executed from memory (e.g., Ganel et al., 2008; Singhal, Culham, Chinellato, & Goodale, 2007; Westwood, McEachern, & Roy, 2001).

The assumption that both perception and delayed action rely on visual processing in the ventral stream allows us to derive different predictions for the *strategy* and *processing hypotheses*. The *strategy hypothesis* assumes that regardless of whether or not a delay is present, the same strategy is applied. Hence, it predicts that the oblique effect will be found for matching but not for posting with and without delay. In contrast, the *processing hypothesis* assumes that posting with delay recruits visual information from the ventral stream. Consequently, it predicts that delayed posting should be subject to the same biases as matching and will thus also be susceptible to the oblique effect.

In a series of three experiments, we tested whether an oblique effect can be found in posting which, in turn, would provide some indication that this task relies on visual orientation processing as previously assumed and can therefore be considered a useful tool to identify dissociations between perceptual and visuomotor processes. In Experiment 1, we used the

classic letter posting and matching paradigm and manipulated the availability of visual feedback (closed-loop vs. open-loop) in both tasks. This experiment served two major purposes. Firstly, we wanted see if we could replicate Gosselin-Kessiby et al.'s (2008) finding that there is no oblique effect in posting. This seems important as their study used versions of the matching and posting tasks that differed in many respects from the posting and matching tasks typically employed in the neuropsychological research on the perception-action model. Hence, we thought it is necessary to first test whether an oblique effect is also absent when a conventional posting task is used. Secondly, several studies have demonstrated that perceptual and visuomotor tasks can be differently affected by the availability of visual feedback (e.g., Franz, Hesse, & Kollath, 2009; Kopiske, Bruno, Hesse, Schenk, & Franz, 2016; Utz et al., 2018). For this reason, we wanted to test if there are systematic differences between matching and posting depending on whether or not visual feedback is available when performing the respective task. This seems particularly relevant as in contrast to most reaching and grasping studies where visuomotor performance is affected more strongly by the absence of visual feedback than perceptual performance (e.g., Franz et al., 2009), the opposite was reported for matching and posting where errors increased more strongly for matching than for posting in an open-loop vision condition (Gosselin-Kessiby et al., 2008).

We found that, independent of visual feedback, the oblique effect occurred reliably in perceptual matching but not in visuomotor posting. Instead, orientation errors in posting seemed to strongly depend on the amount of required card/hand rotation in a given trial (i.e., the biomechanical effort involved). As this was a somewhat unexpected observation, we conducted Experiment 2 to further investigate this finding and to establish to what extent matching and posting are affected by biomechanical task demands as those may potentially obscure the presence of an oblique effect in posting. This experiment confirmed a strong effect of rotation requirements on posting but not on perceptual matching. In the context of the present study, the presence of biomechanically induced errors during posting is a concern as they may potentially mask the presence of an oblique effect. It was therefore paramount that we developed a posting task where we accounted for the confound between slot-orientations and rotation requirements. We achieved this in Experiment 3 by adjusting the start-orientation of the hand relative to the slot orientation such that a similar amount of hand-rotation was required for all slot-orientations. As a result of this manipulation, errors in posting were substantially reduced but still no oblique effect emerged. The same manipulation had little effect on the distribution of errors in matching where we still obtained clear evidence of an oblique effect.

The second purpose of Experiment 3 was to test if the oblique effect emerged in posting when a delay was introduced between slot-presentation and movement initiation. The processing account assumes that vision for delayed action is processed in the ventral stream and therefore subject to the same illusions and biases as perceptual performance. But we found that the oblique effect failed to emerge in delayed posting.

Taken together, these findings suggest that the errors found in matching and posting have different causes. Matching errors reflect a perceptual bias (i.e., the oblique effect), whereas posting errors are determined by biomechanical task demands even after delay, when ventral-stream processing should have led to perceptual biases according to the *processing hypothesis*. The finding that oblique effects do not occur in posting in both no-delay and delay-conditions is in line with the *strategy hypothesis* but contradicts the *processing hypothesis'* prediction.

Experiment 1

In Experiment 1, we tested whether an oblique effect exists and is of comparable size in standard posting and matching tasks. In the posting task, participants posted a card in a slot. In the matching task participants matched the card's orientation to the slot (cf. Figure 1B). Tasks were performed with full vision (visually closed-loop) and without vision (visually open-loop) of the hand and the posting device during the movement (Figure 1 C) in order to determine if and how the availability of visual feedback affected orientation errors during posting and matching.

Methods

Participants

Twenty right-handed undergraduate and postgraduate students of the University of Aberdeen (5 male) aged between 19-29 years (M=23 years, SD=2.7) participated in this experiment. They all had normal or corrected-to-normal visual acuity. All participants provided informed written consent before participation and were reimbursed with £10. The study was approved by the Psychology Ethics Committee (PEC/3901/2018/5) of the University of Aberdeen.

Apparatus and Stimuli

The letter posting apparatus consisted of a vertical wooden panel (60 x 60 cm) with a central removable wooden disk (diameter: 40 cm) placed in front. The disk had a central rectangular cut-out (12 cm x 3 cm) that served as the posting slot. The disk could be removed and attached in different orientations on the vertical panel using pins thereby allowing quick and accurate

changes in slot orientation on a trial-by-trial basis. The whole apparatus was placed on top of a standard table (see Figure 1B, the apparatus is also described in detail in *Hesse and Schenk (2014)*). The centre of the letter-posting slot was about 30 cm above the table top and was presented in four different orientations 0° (vertical), 22.5°, 45° (diagonal), and 90° (horizontal) rotated in clockwise direction from vertical orientation. The posting object was a green Perspex card with a size of 11.5 x 8 cm and a thickness of 1 cm that weighed 104 g. The card's resting positon was a slanted wooden block with an average height of about 5 cm (Figure 1B). The top surface of the start object was slightly slanted about 102 degrees clockwise from the vertical orientation. The set-up and the way participants were instructed to hold the card at the start block ensured that they always rotated the card in counterclockwise direction to reach any of the slot orientations during both posting and matching (i.e., 12 degrees to reach the horizontal slot and 102 degrees to reach the vertical slot). The distance between the centre of the start position and the centre of the posting slot was about 40 cm (26 cm above the table surface [z-direction] and 30 cm in the fronto-parallel plane [y-direction]).

Two infrared light-emitting diodes were attached to the two front edges of the Perspex card to record its position and orientation in 3D space using an Optotrak 3020 system (Northern Digital Incorporation, Waterloo, Ontario, Canada) at a sampling rate of 200 Hz. Prior to the experiment, the Cartesian coordinate system of the Optotrak was calibrated and aligned to the table top plane. Throughout the experiment, participants vision was controlled using liquid-crystal shutter glasses (PLATO Translucent Technologies, Toronto, Ontario, Milgram, 1987). Experiments were programmed in MATLAB using the custom-built Optotrak Toolbox (Franz, 2004).

Procedure

Participants sat at a table in a well-lit room in front of a posting device. They were asked to adjust the chair in height so they could comfortably hold the card at the centrally aligned start position and were able to reach the slot for posting. They held the card in their dominant right hand with the thumb placed on top of the card (allowing comfortable and easy counterclockwise rotation). Each trial started with participants placing the card on top of the slanted surface of the start position. After the shutter glasses had closed, the experimenter removed the disk from the posting device and placed it back with the slot at the required orientation. Note that the experimenter removed and re-attached the posting disk in every trial (even when the slot orientation remained unchanged). Thus, there were no auditory cues for

the participant about the upcoming orientation of the slot. Once the disk was attached in the desired orientation, the experimenter started the trial manually with a keypress. Following the keypress, the shutter glasses opened for a preview period of 1 second. During this period, participants were instructed to view the slot in front of them but to wait with their movement until an auditory go-signal (1000 Hz, 100 ms) was presented. In response to the go-signal, participants performed either a perceptual matching task or a visuomotor posting task either under full vision (closed-loop) or without visual feedback (open-loop). Both task and viewing conditions were blocked and counterbalanced across participants (see Figure 1C). Half the participants started with the matching tasks and the other half with the posting tasks and half started with the visually open-loop vision condition and the other half with the visually closed-loop vision condition.

In the posting task, participants had to move the card from the start position to the slot and pass the card's front edge through it. Subsequently, they moved the card back to the start position. In the visually closed-loop vision conditions, the glasses remained open for the whole movement so that participants could see both their hand and the slot during posting. In the visually open-loop conditions, the shutter glasses closed once one of the markers on the card had been lifted by more than 25 mm in height (z-direction) from the start position. Thus, occlusion of vision was triggered by the card's movement and participants had to finish their movement without visual information about their surroundings. In order to prevent learning effects from potential haptic feedback in the open-loop conditions, participants were instructed to move the card towards the slot in one swift movement. As soon as they collided with the panel, they were instructed to move their hand back to the start position without making any further attempts of posting the card through the slot.

In the matching task, participants held a response button in their left hand. At the go-signal, they moved the card to the right, roughly above a green paper cross glued to the table top (positioned about 20 cm to the right in the x-direction and 10 cm in front, i.e., y-direction, of the start position) and indicated/matched the orientation of the slot as accurately as possible at this position. Note that as long as participants roughly moved their hand to the right of the slot and slightly forward matching responses were recorded. The aim of having the matching task performed at a different position (i.e., go the right of the slot) was to prevent participants from being able to visually line up the card to the slot orientation in the full-vision conditions. Once they thought the card matched the slot's orientation, they pressed the response button held in their left hand. If the resultant velocity of the card markers exceeded 3 cm/s at the moment the

button was pressed, participants were informed that they needed to keep the card still during matching and the trial was recycled and repeated later during the experiment. As for posting, matching was performed visually closed-loop and visually open-loop.

In all tasks, participants had 3 seconds to execute their movements after which the Optotrak stopped recording (and in the visually closed-loop condition shutter glasses would close at this point). If participants did not finish their movements during this interval, the trial was classified as error and repeated at a randomly selected later position in the trial sequence. All slot orientations were presented pseudo-randomly and repeated eight times, resulting in 32 trials per block and 128 trials in total. Three practice trials preceded each block. Participants were asked to be as accurate as possible during posting and matching but did not receive any explicit instructions about movement speed.

Data analysis

To determine the card's resultant velocity, we first computed the virtual midpoint (in 3D) between the two markers placed on the card's front edge (Hesse et al., 2011). Velocity was then calculated from the 3D position data of this virtual midpoint along the movement path (i.e., for every frame). Movement onset was defined as the moment in time when the resultant velocity exceeded a velocity threshold of 5 cm/s. For posting, we defined the end of the movement as the moment when one of the markers became invisible (i.e., the front edge of the card went through the slot). As during visually open-loop posting, participants did not always manage to post the card successfully through the slot, we used an alternative criterion to determine the end of movement in those cases. Specifically, we determined the frame with the lowest velocity of the card in close vicinity of the slot (i.e., less than 40 mm in y-direction). We used this criterion only for preliminary data checks, i.e., to determine how much card rotation took place at the end of the movement (see below and Figure 1A) and at which moment in time the card had reached a stable orientation prior to hitting the panel. Card orientation was determined in 2D space as projected onto the plane of the slot-board facing the participant. A 12 o'clock vertical orientation was defined as 0° and a 3 o'clock horizontal orientation as 90°. Using those criteria, Figure 1A shows that participants reached the final card orientation at around 65-80% of their movement. Hence, consistent with previous literature on hand movements, most of the required hand/card rotation was achieved during the first half of the movement (see Hesse & Deubel, 2009). To ensure participants had not yet hit the panel (and had not received any haptic feedback about the correctness of the card orientation), we

determined the final card orientation at the moment in time when the virtual midpoint of the front edge of the card was 50 mm away from the target slot in y-direction (on average occurring at about 75-80% of the posting movement). In the matching task, the final matching orientation was determined as the moment participants pressed the response button (and the card was held sufficiently still, see above). We calculated the absolute (i.e., unsigned) and the directional (i.e., signed) errors[1] as the deviation from the actual slot orientation in both posting and matching.
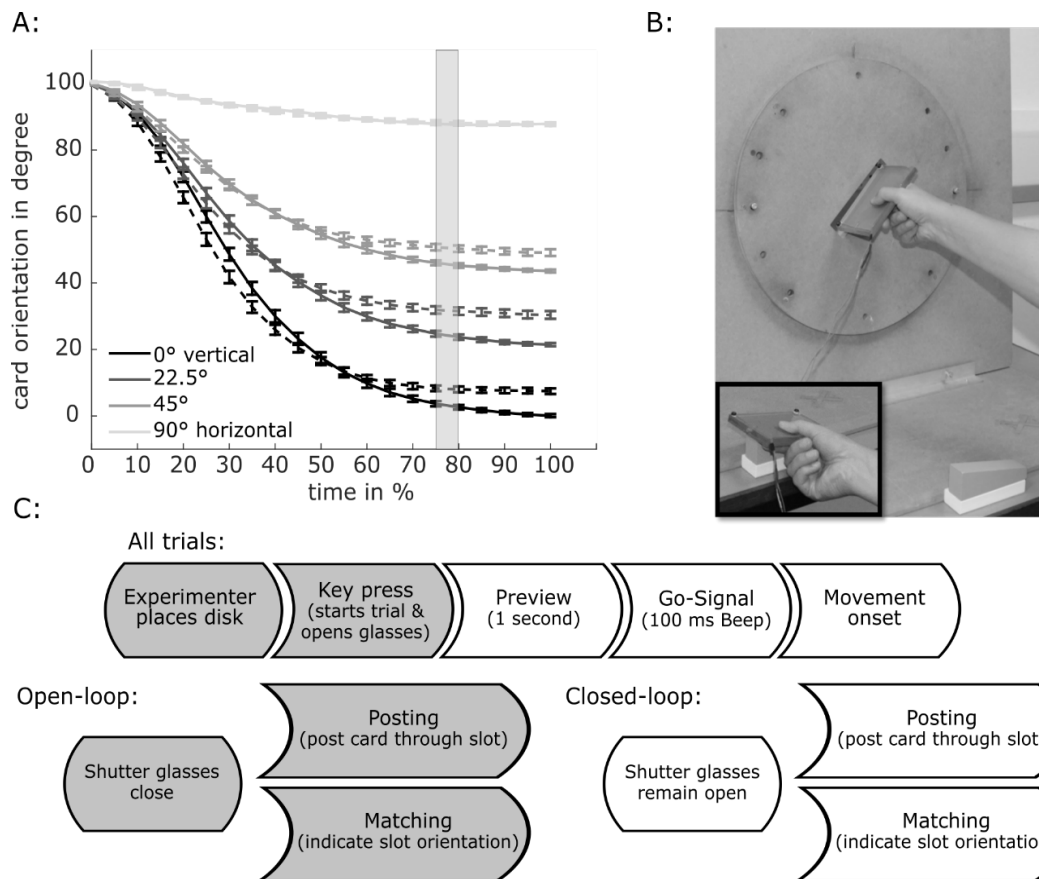

Figure 1: A) Average rotation of the card from movement onset (0%) until the end of movement (100%, see Methods section for details) for the four different slot orientations. Solid lines are movements in the visually closed-loop condition and dashed lines in the visually open-loop conditions. The end orientation of the card was determined when the virtual midpoint of the card was 5 cm away from the slot in fronto-parallel plane. On average, this was the case at about 75-80% of the defined movement path (grey shaded area). Error bars indicate ± 1 SEM (between subjects). B) Photograph of the letter-posting device used in all Experiments and the start block used in Experiment 1. Participants were instructed to hold the card as shown in the inset of the figure ensuring that the card was always turned in counterclockwise direction for all slot orientations. C) Illustration of the trial sequence. Grey shaded fillings indicate the absence of vision and white fillings the presence of vision during the task.

---

[1] We use those measures to be comparable to the literature, where those measures are traditionally used (e.g., Gosselin-Kessiby et al., 2008). Consider we measured an orientation $\varphi_{measured}$, while the true orientation was φ_{true}. Then the absolute error is $|\varphi_{measured} - \varphi_{true}|$ and the directional error is $\varphi_{measured} - \varphi_{true}$. The absolute error therefore reflects the absolute deviation from the true value (independent of its direction), while the directional error preserves the direction of the deviation.

Data analysis was performed in SPSS using repeated measures analysis of variance (ANOVA) and applying Greenhouse-Geisser corrections when applicable (Greenhouse & Geisser, 1959). Values are presented as means ±1 standard error of the mean (between subjects). *Post-hoc* contrasts were carried out using Bonferroni correction. A significance level of alpha = 0.05 was used for all statistical analyses.

Results and Discussion

Figures 2A and 2B show the absolute orientation errors (used to determine the existence of an oblique effect) for both matching (Fig. 2A) and posting (Fig. 2B) as a function of slot orientation and vision condition. We initially analysed all data using a 2 (task) x 2 (vision condition) x 4 (slot orientation) repeated measures ANOVA. This analysis revealed a significant two-way interaction between task and slot orientation, $F(3,57)=12.76$, $p<.001$, $\eta_p^2=0.40$, as well as a significant three-way interaction between all variables, $F(3,57)=3.25$, $p=.028$, $\eta_p^2=0.15$. Thus, we followed this analysis up with separate 2 (vision conditions) x 4 (slot orientation) repeated-measures ANOVAs conducted for matching and posting respectively.

For the *matching task*, both main effects of vision, $F(1,19)=48.30$, $p<.001$, $\eta_p^2=0.72$, and slot orientation, $F(3,57)=20.48$, $p<.001$, $\eta_p^2=0.52$, were highly significant with a significant interaction between them, $F(3,57)=8.03$, $p<.001$, $\eta_p^2=0.30$. Importantly, post-hoc tests conducted for each vision condition separately, confirmed that absolute errors were consistently smaller for the two cardinal slot orientations (vertical and horizontal) than for the two oblique orientations tested (*all p<.03,* Bonferroni corrected) but did not differ significantly from each other (both p=1). Similarly, there was no difference in the size of the absolute error between the two oblique orientations in the visually closed-loop vision condition (p=1). However, in the visually open-loop condition, errors were larger for the 22.5° slot orientation than for the 45° orientations (*p=.008,* Bonferroni corrected) indicating that the oblique effect was less pronounced for the diagonal angle than for the 22.5° oblique orientation (see Figure 2A). In summary, the oblique effect, as indicated by smaller absolute errors for cardinal than oblique slot orientations, occurred consistently in the matching task and was more prominent when visual feedback was unavailable.

The same analysis for the *posting data* revealed again, significant main effects of vision condition, $F(1,19)=50.21$, $p<.001$, $\eta_p^2=0.73$, and slot orientation, $F(3,57)=32.33$, $p<.001$, $\eta_p^2=0.63$, as well as a statistically significant interaction between them, $F(3,57)=17.99$, $p<.001$, $\eta_p^2=0.49$. Post-hoc tests revealed a significant linear effect of slot orientation on absolute errors in the visually closed-loop condition, $F(1,19)=6.15$, $p=.02$, $\eta_p^2=0.25$, but with pairwise comparisons not being statistically significant (all $p>.17$, Bonferroni corrected). For the visually open-loop vision condition, errors increased overall as compared to the visually closed-loop condition and were largest and of similar size in the vertical (0°) and 22.5° slot orientations ($p=.40$) and smallest for the horizontal slot orientation (all p<.001, see Figure 2B).
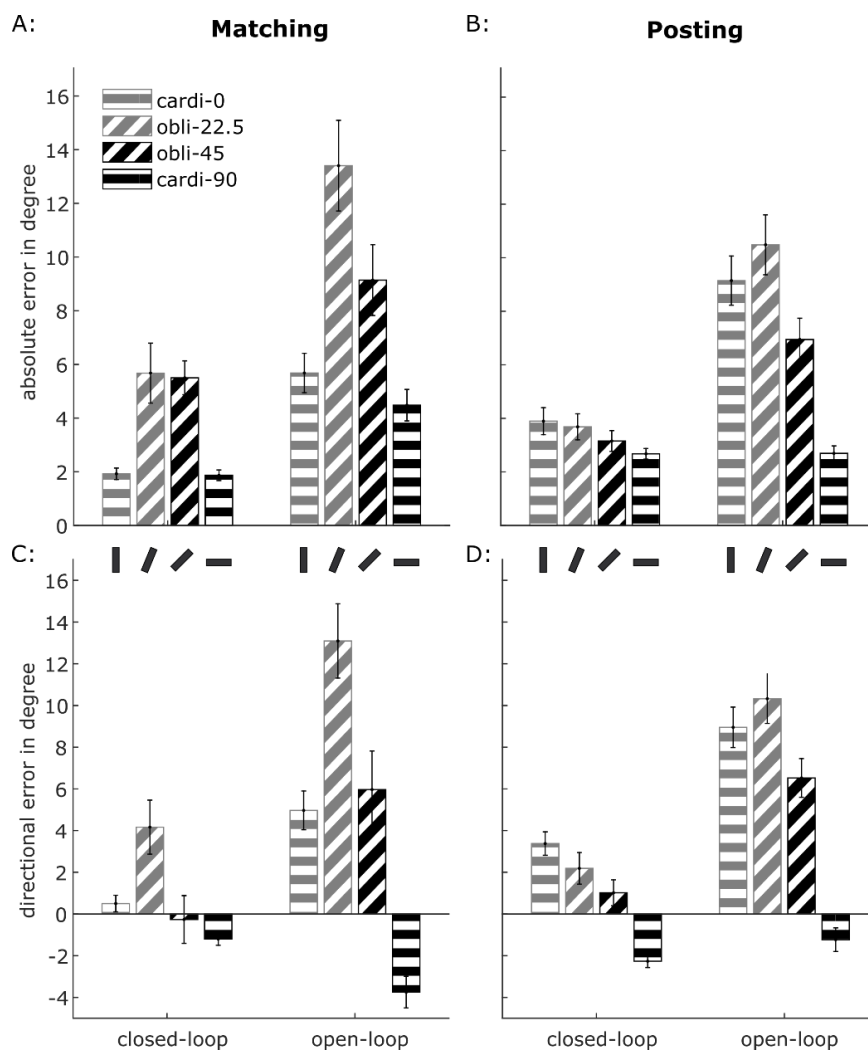

Figure 2: Absolute orientation errors (A and B) and directional orientation errors (C and D) as a function of slot orientation and vision condition in matching (A and C) and posting (B and D). The black bars indicate the orientation of the slot. Absolute errors indicate a clear oblique effect for matching but not for posting. Directional errors indicate a bias towards the start orientation of the hand in posting but not in matching. Positive values indicate clockwise and negative values counterclockwise directional errors. Error bars indicate ±1 SEM (between subjects).

This pattern of results does not suggest the existence of an oblique effect during posting. At first glance, the finding that posting errors are larger for vertical orientations than diagonal and horizontal ones may seem quite counterintuitive, however, considering the specific task demands it may come less as a surprise. Recent research has consistently shown that humans prefer to execute movements in a way that minimises effort and biomechanical costs (e.g., Cos, Bélanger, & Cisek, 2011; Cos, Medleg, & Cisek, 2012; Rosenbaum & Gaydos, 2008; Rosenbaum & Gregory, 2002). As participants started their movements with the card placed on a slightly tilted start position (102°, i.e. approx. 4 o'clock, Figure 1B); posting the card in a horizontal orientation required the smallest amount of (counterclockwise) rotation. Rotation requirements successively increased for 45°, 22.5° and 0° slot orientations. Consequently, if participants aim to minimise the amount of hand/card rotation, errors should increase with the amount of rotation required. This should become visible in the directional orientation errors which should reveal a counterclockwise bias towards the start orientation in the posting task but not in the matching task. To test if this was the case, we also calculated the directional errors for all conditions and analysed the data in the same way as for the absolute error.

Figures 2C-D shows the directional errors for both matching (Fig. 2C) and posting (Fig. 2D) tasks as a function of slot orientations and for both vision conditions. As the initial 2 (task) x 2 (vision condition) x 4 (slot orientation) repeated-measures ANOVA revealed again a significant three-way interaction, $F(3,57)=4.38$, $p=.008$, $\eta_p^2=0.19$, indicating that vision and slot orientation affected posting and matching differently, we followed this analysis up with separate 2 (vision conditions) x 4 (slot orientation) repeated-measures ANOVAs conducted for matching and posting respectively.

For the *matching task*, both main effects of vision, $F(1,19)=31.84$, $p<.001$, $\eta_p^2=0.63$, and slot orientation, $F(3,57)=31.06$, $p<.001$, $\eta_p^2=0.62$, were significant with a significant interaction between them, $F(3,57)=27.25$, $p<.001$, $\eta_p^2=0.59$. Overall, directional errors were larger in matching when visual information was unavailable. With full vision available, participants primarily made clockwise errors for the 22.5° slot orientation (i.e., towards the diagonal) while directional errors were negligible for all other orientations tested. Without visual feedback, clockwise errors increased for the 22.5° slot orientation and also occurred, but to a smaller extent, for the vertical and 45° slot orientations. Yet, the fact that clockwise errors were significantly smaller for the vertical slot orientation (requiring a larger amount of

counterclockwise rotation) than for the 22.5° orientation suggests that these directional errors were not driven by rotational requirements (see Figure 2C).

The same analysis conducted for the directional errors in the *posting conditions* again revealed significant main effects of vision, $F(1,19)=50.53$, $p<.001$, $\eta_p^2=0.73$, and slot orientation, $F(3,57)=58.31$, $p<.001$, $\eta_p^2=0.75$, with a significant interaction between them, $F(3,57)=22.34$, $p<.001$, $\eta_p^2=0.54$. Again, directional errors were overall larger when visual feedback was unavailable. More to the point, in the visually closed-loop condition, the clockwise error (in the direction of the start orientation) increased linearly with increased rotation requirements. This pattern was generally similar for the visually open-loop condition, with the largest counterclockwise errors for the vertical (0°) and 22.5° slot orientations. In summary, the data pattern seems broadly consistent with the assumption that errors in posting are biased towards the start orientation and depend on the amount of hand/card rotation required (see Figure 2D).

In sum the findings of the experiment confirm that a common perceptual bias in orientation perception, i.e. the oblique effect (Appelle & Gravetter, 1985; Campbell et al., 1966; Mikellidou et al., 2015; Vogels & Orban, 1985), consistently affects judgments in a perceptual matching task but does not seem to affect visuomotor posting performance. This was the case regardless of whether or not visual feedback was available during movement execution. Importantly, we observed that error patterns in posting seemed to be primarily determined by the amount of required hand rotation (i.e., biomechanical effort). In particular, the analysis of the directional errors indicated that in posting, but not matching, participants tend to keep a card orientation that is biased towards the start orientation of their hand. The perceptual matching task usually strongly emphasises accuracy with participants being instructed to indicate/match the orientation of the slot as accurately as possible. This strong emphasis on orientation-matching accuracy discourages participants to trade off accuracy against effort. Consequently, the involved effort of the movement should be largely irrelevant for performance in the matching task. In contrast, for posting, participants are instructed to post the card successfully through the letter slot. This requires them to rotate the card such that its edges safely clear the edges of the posting slot. In the setup described here, participants are able to post the card successfully within about 15° of the actual slot-orientation. This allows for a range of successful hand-orientations and thereby provides room for adjusting the posting-movement to minimise effort. Consequently, we expect that biomechanical effort plays a greater role in posting as compared to matching. The observation that during posting participants aim to reduce biomechanical effort, is consistent with a large amount of evidence

from motor control literature suggesting that humans aim to select and perform movements that are safe and efficient and minimise the biomechanical and energetic costs and thus the immediate effort involved in the action (Cohen, Biddle, & Rosenbaum, 2010; Hesse, Kangur, & Hunt, 2020; Rosenbaum & Gaydos, 2008; Rosenbaum & Gregory, 2002; Ross, Schenk, & Hesse, 2014).

Furthermore, the finding that directional errors increase with the amount of rotation required is also consistent with the assumption that the posting task does not necessarily rely on orientation information but rather constitutes an obstacle avoidance task thereby supporting the *strategy hypothesis* (Hesse et al., 2011). However, as the hypothesis that orientation errors in posting primarily depend on biomechanical rotation requirements (and thus biomechanical effort) was formulated after seeing the data, we first aimed to test this hypothesis much more directly in an additional experiment. This is also essential, as large biomechanical effects may possibly mask the existence of an oblique effect in posting and hence will need to be accounted for when testing for the existence of an oblique effect in posting. To determine how rotational effort affects orientation errors in posting and matching, we varied the card's start orientation in Experiment 2 and let participants perform the same matching and posting tasks as in Experiment 1. We predicted that posting errors would increase with the amount of card rotation required and thus vary for the different slot orientations depending on the start orientation of the hand. In contrast, we expected no effects of start orientation on the orientation errors in the perceptual matching task.

Experiment 2

In Experiment 1, we found a clear oblique effect in matching. However, the error pattern observed in the posting condition suggested the influence of biomechanical demands and rotational effort. To test this observation more directly, we varied the card's start orientation and thus the rotational effort involved in posting the card in the different slot orientations. We hypothesised that start orientation has little effect on the orientation errors in the matching task because participants were instructed to match the slot as accurately as possible. In contrast, in the posting task, participants might attempt to minimise rotational effort, while still being able to perform the task successfully (i.e., post the card in the slot). Hence, we expect the variation of the start orientation to affect posting but not matching. We employed a full-vision condition, to minimise chances of participants colliding with the posting panel thereby potentially obtaining additional haptic feedback on their posting performance.

Methods

Participants

Twenty-one right-handed undergraduate and postgraduate students of the University of Aberdeen (4 male) with normal or corrected-to-normal visual acuity, who had not previously participated in Experiment 1, were recruited for this experiment. One female participant was excluded as she failed to keep the card consistently at the right orientation at the start position. The remaining twenty participants were aged between 19-33 years (M=23 years, SD=3.2). All participants provided informed written consent prior to participation and were reimbursed with £10. The study was approved by the Psychology Ethics Committee (PEC/4223/2019/5) of the University of Aberdeen.

Apparatus, Stimuli, Procedure and Data analysis

The apparatus, setup, stimuli and general procedure were identical to Experiment 1. However, all posting and matching movements were now performed with full vision available (visually closed-loop). In Experiment 1, the card's orientation at the start position was standardised and kept identical for all trials and conditions. In this experiment, we varied the card's start-orientation (see Figure 3). The start-orientation was either vertical (0°) or diagonal (45°). Start orientations were blocked and counterbalanced across participants. Half the participants started with the vertical start orientation and the other half with the diagonal start orientation. As previously, half the participants started with the matching task and the other with the posting task. Slot orientations were presented pseudo-randomly within each block. Again, each slot orientation was presented eight times, resulting in 32 trials per block and 128 trials in total. Data was processed in the same way as in Experiment 1.
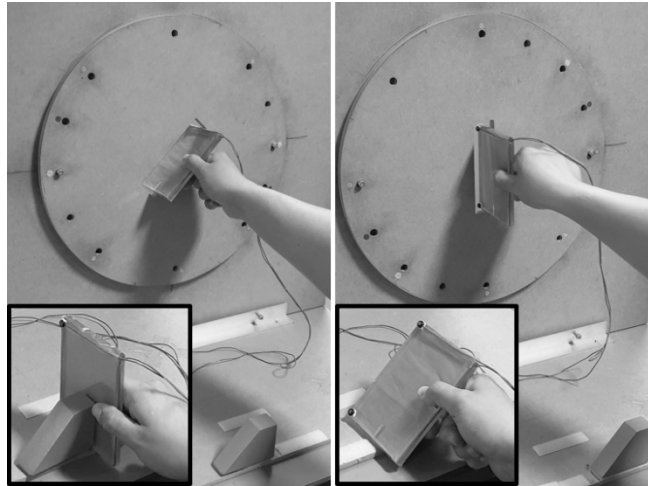
Figure 3: Photograph of the posting device with the start blocks used in Experiment 2. The insets show the placement of the card prior to movement onset. A wooden block was used to ensure participants held the card in the correct orientation prior to movement onset. The position of the start block was shifted between blocks to ensure the start position was always centrally aligned with the posting panel. Left panel: Start orientation vertical and posting slot diagonal. Right panel: Start orientation diagonal and posting slot vertical.

Results

Figures 4A and 4B shows the absolute orientation errors for all slot orientations as a function of start orientation (vertical vs. diagonal) separately for matching and posting. Descriptively, and consistent with an oblique effect, absolute orientation errors were consistently larger for oblique orientations than for cardinal orientations in the perceptual matching task (Figure 4A). However, in the posting task, this error pattern clearly differed (Figure 4B).

If, as we predicted, biomechanical considerations determine posting errors, i.e., depending on the amount of rotation required during the movement, errors should be smallest in conditions in which the card has to be rotated the least and increase with larger rotation requirements. Consequently, errors for the different slot orientations should vary with the start orientation of the hand. Specifically, for the vertical start orientation, errors should be smallest for the vertical slot orientation and should increase successively for the 22.5°, 45° and horizontal slot orientations. For the diagonal start orientation, errors should be smallest for the same 45° slot orientation and largest for the two cardinal orientations. Further, the directional errors should show consistent biases in direction of the start orientation. In contrast, errors in matching are not expected to vary with the hand/card's start orientation.

We initially analysed all data using a 2 (task) x 2 (start orientation) x 4 (slot orientation) repeated measures ANOVA. As predicted, this analysis revealed significant three-way

interaction effects for both absolute errors, $F(3,57)=7.43, p<.001, \eta_p^2=0.28$, and directional errors, $F(3,57)=3.99, p=.012, \eta_p^2=0.17$. We followed this analysis up with separate 2 (start orientation) x 4 (slot orientation) repeated-measures ANOVAs, conducted for matching and posting respectively.

For the absolute error in the *matching task*, this analysis revealed a significant main effect of slot orientation, $F(3,57)=24.73, p<.001, \eta_p^2=0.57$, but neither a main effect of start orientation ($p=.15, \eta_p^2=0.10$) nor an interaction effect between the two factors ($p=.22, \eta_p^2=0.07$). In line with the existence of an oblique effect, the absolute orientation errors were significantly smaller for both cardinal slot orientations than for the two oblique orientations (all $p<.001$). Furthermore, absolute errors were of similar size for the two cardinal slot orientation ($p=.56$) and the two oblique slot orientations ($p=.1$). As predicted, there was no effect of start orientation on the absolute matching errors.

The same analysis for the absolute errors in the *posting task* confirmed statistically significant main effects of both, slot orientation $F(3,57)=6.02, p=.001, \eta_p^2=0.24$, and start orientation, $F(1,19)=5.41, p=.03, \eta_p^2=0.22$, as well as a significant interaction effect between them, $F(3,57)=18.34, p<.001, \eta_p^2=0.49$. Thus, in posting, absolute orientation errors for the different slot orientations depended on how the card was oriented at the start of the movement. When participants held the card in a vertical orientation, absolute errors were smallest for the 0° and 22.5° slot orientations requiring the smallest amount of hand rotation and increased with the amount of rotation needed in the 45° and 90° slot orientation conditions (see Figure 4B). In contrast, for the diagonal (45°) start orientation, the absolute error was smallest if the card had to be posted in the same (diagonal) orientation and increased again with the amount of required hand rotation. These findings confirm that, as predicted, orientation errors increase with the amount of required hand rotation in the posting, but not in the matching task. If we assume, that this is a consequence of an action strategy that minimizes the amount of biomechanical effort involved in posting, we further predicted that the directional rotation errors would show a bias towards the start orientation of the hand. Directional errors are shown in Figures 4C-D.
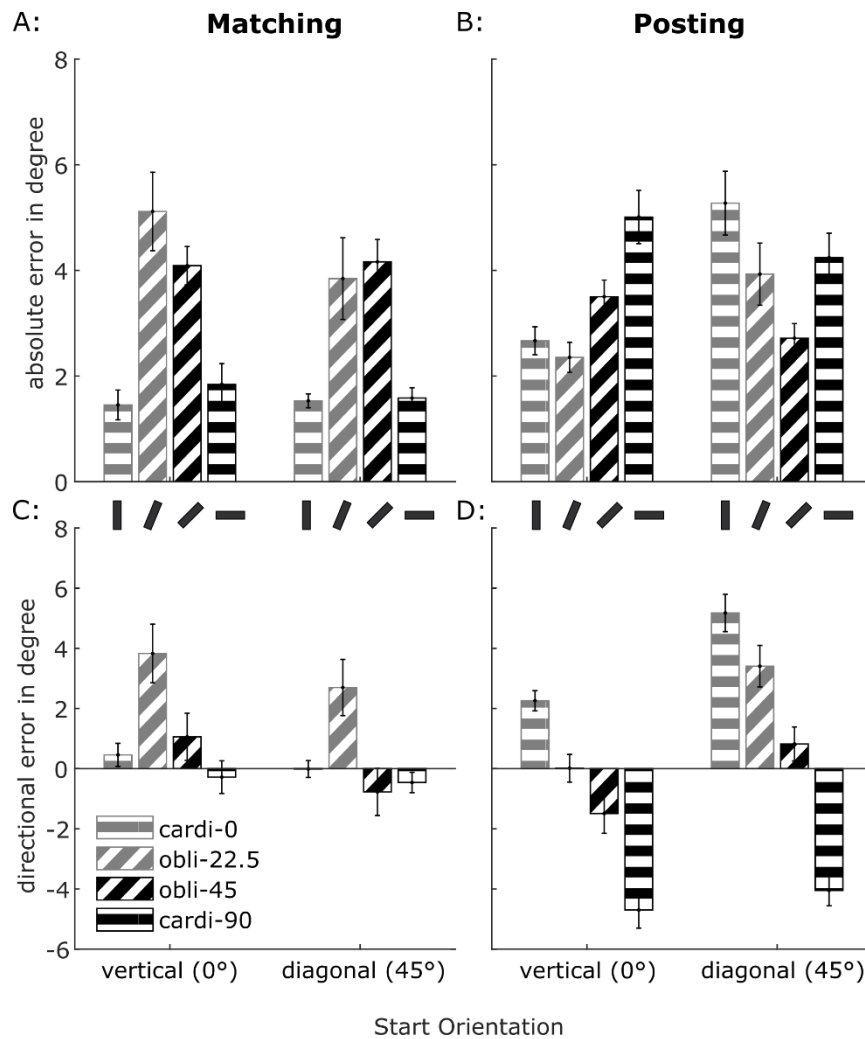
Figure 4: Absolute orientation errors (A and B) and directional orientation errors (C and D) as a function of slot orientation and start orientation in matching (A and C) and posting (B and D). The black bars indicate the orientation of the slot. Absolute errors indicate a robust oblique effect for matching. In contrast, for posting, errors primarily depend on the start orientation of the hand, increase with the amount of hand rotation required (B), and are biased towards the start orientation of the hand (D). Positive values indicate clockwise and negative values counterclockwise directional errors. Both tasks were conducted visually closed-loop. Error bars indicate ±1 SEM (between subjects).

Regarding, the directional errors in the *matching* task, the ANOVA revealed significant main effects of start position, $F(1,19)=8.58$, $p=.009$, $\eta_p^2=0.31$ and slot orientation $F(3,57)=8.96$, $p=.001$, $\eta_p^2=0.32$, with no interaction between the two factors ($p=.26$, $\eta_p^2=0.06$). Post-hoc tests showed that there were slightly larger clockwise errors for the vertical start orientation ($1.3° \pm 0.41°$) than for the diagonal start orientation ($0.4° \pm 0.38°$). Regarding the effect of slot orientation, participants again tended to overestimate the orientation of the $22.5°$ slot

orientation making consistent clockwise errors while directional errors in the three remaining conditions were smaller and did not differ significantly from each other (Figure 4C).

The 2 (start orientation) x 4 (slot orientation) repeated-measures ANOVA conducted on the directional errors in the *posting condition*, confirmed again significant main effects of both start orientation, $F(1,19)=26.23$, $p<.001$, $\eta_p^2=0.58$, and slot orientation $F(3,57)=60.19$, $p<.001$, $\eta_p^2=0.76$, as well as a significant interaction between them, $F(3,57)=5.36$, $p=.008$, $\eta_p^2=0.22$. The interaction effect confirms that, as expected, directional errors for the different slot orientations varied depending on the hand's start orientation. As depicted in Figure 4D, directional errors changed linearly in both start conditions. In the diagonal start orientation condition, the directional errors were, as predicted, smallest when the card had to be posted in the same diagonal 45° slot orientation. For the 22.5° and vertical (0°) slot orientations, participants made clockwise errors (i.e. towards the 45° start orientation), and for the horizontal (90°) slot orientation they made counterclockwise errors (i.e., again biased towards the start orientation). The same trend of increased directional errors for target orientations further away from the start orientation was also found for the vertical start orientation (i.e., increased counterclockwise errors for 45° and 90° slot orientations). Somewhat surprisingly, the directional error was smallest for the 22.5° slot orientation with a small clockwise error in the vertical slot orientation conditions. This clockwise bias for vertical posting probably reflects a known preference of the hand to maintain a slight rightward orientation in a relaxed state (Kleinholdermann, Franz, & Gegenfurtner, 2013; Lederman & Wing, 2003). Overall, this pattern of results suggests that during posting, but not matching, the final hand and card orientations, and hence the associated absolute and directional errors, depend on the hand's start orientation. It seems that the hand posture is selected to minimise the amount of rotation required, thereby decreasing the effort and increasing the comfort of the movement (Rosenbaum & Gaydos, 2008).

In summary, this pattern of results suggests that rotation requirements and biomechanical demands affect orientation errors in the posting but not in the matching task. This is consistent with the idea that different strategies are used to perform the two tasks that pose different demands on participants (i.e., indicating orientation as precisely as possible vs. safely posting the card without collision) which in turn means that different types of visual information are relevant when performing the two tasks.

However, our findings still leave a couple of important questions unanswered. Firstly, one could argue that oblique effects are also present in posting but may have been masked by the

larger errors related to the biomechanical task demands. Secondly, the absence of an oblique effect in posting could also be interpreted as evidence for the processing hypothesis predicting that visuomotor orientation representations are more precise and distinct from perceptual orientation representations (Milner & Goodale, 1995, 2006).

We aimed to address both questions in Experiment 3. To determine if rotation requirements and biomechanical demands masked potential perceptual influences, we minimised the differences in the rotation requirements for all slot orientations by adjusting the hand's start orientation on a trial-by-trial basis. We expected that by doing so differences between orientation errors for different slot orientations would be attenuated thereby making it more likely to reveal any putative oblique effect in posting. Furthermore, to determine if posting may rely on visual representations of orientation that are different (and potentially more accurate) than those used for the perceptual matching task, we conducted posting and matching (with comparable rotation requirements for all slot orientations) in two different conditions: immediate movements and delayed memory-guided movements.

Within the perception-action literature, it has consistently been argued that executing movements after delay and without concurrently available visual information causes a shift from visuomotor (dorsal) processing mode to the ventral (perceptual) processing mode (e.g., Goodale et al., 2005; Goodale et al., 2004; Milner et al., 2003; Westwood, Heath, & Roy, 2003). According to this assumption, introducing a delay between the presentation of the perceptual information and the onset of the movement should force the visuomotor system to rely on the stored visual information that is also used for performing the equivalent perceptual task. Consequently, perceptual biases that are often not found in immediate action tasks are expected to emerge in delayed action tasks (Ganel et al., 2008; Singhal et al., 2007; Westwood & Goodale, 2003). To test this, we introduced a memory delay of 1 second. Such a delay presumably shifts the visuomotor system into memory-guided mode, thereby forcing the motor system to recruit its visual input from the ventral stream (Goodale et al., 2004).

Experiment 3

This experiment served two major purposes. Firstly, we wanted to determine if the oblique effect can be observed in posting when rotation requirements (and thus biomechanical effort) are comparable for cardinal and oblique slot orientations. Secondly, we wanted to test if the oblique effect emerges in a delayed posting task. The findings from this experiment will allow

us to distinguish between the predictions of the *strategy* versus *processing hypothesis*. The *processing hypothesis* would predict that posting after delay shows similar biases as matching (i.e., presence of an oblique effect) and different biases than posting under full vision. In contrast, the *strategy hypothesis* would predict no oblique effects in posting, independent of delay and that errors in posting and matching differ in both immediate and delayed conditions (see Table 1).

Table 1

Predictions	Absolute orientation errors for cardinal and oblique slot orientations	
	Matching vs delayed posting	*Posting vs delayed posting*
Processing Hypothesis	Similar	Different
Strategy Hypothesis	Different	Similar

Table 1. Predictions of the two contrasting hypotheses regarding the effect of delay on absolute orientation errors (as an indicator of the oblique effect) for cardinal and oblique slot orientations in posting and matching.

Methods

Participants

Thirty-six right-handed undergraduate and postgraduate students of the University of Aberdeen (8 male) with normal or corrected-to-normal visual acuity were recruited for this experiment. The availability of visual information (i.e., full-vision immediate vs. visually open-loop 1-s delay) was manipulated between subjects. From the 18 participants completing the full vision condition (4 male), two female participants were excluded from data analysis, as they could neither keep the card steady nor at the correct orientation at the start position during the preview period. The remaining sixteen participants were between 19-26 years (M=22 years, SD=1.9). The eighteen participants completing the delay condition were between 19 and 34 years (M: 23.3, STD: 3.1 years). All participants provided informed written consent prior to participation and were reimbursed with £6. The study was approved by the Psychology Ethics Committee (PEC/4223/2019/5/upd/956) of the University of Aberdeen.

Apparatus, Stimuli, Procedure and Data analysis

The apparatus, setup, stimuli and general procedure were similar to Experiments 1 and 2. However, we now varied the start-orientation on a trial-by-trial basis. Specifically, the start block was built such that participants could rest the card prior to posting or matching at an

orientation that always required them to rotate the card by 22.5° in clockwise direction. That is, for the 0° (vertical), 22.5°, 45° and 90° (horizontal) slot orientations, the start orientations of the hand were -22.5°, 0°, 22.5° and 67.5° respectively (see Figure 5). To ensure that the card rested correctly and at the correct orientation, the experimenter would adjust the start block and carefully guide the participant's hand to the resting position (while shutter glasses were closed). Thus, in every trial, the experimenter (KB) changed both the slot orientation and the start block orientation. As previously, half the participants started with the matching task and the other with the posting task. Slot orientations were presented pseudo-randomly within each block. Each slot orientation was presented ten times, resulting in 40 trials per block and 80 trials in total.

One group of participants performed the task with full-vision available (similar to Experiment 2). That is, after the experimenter had placed their hand at the start block and adjusted the target disk, shutter glasses opened for a 1 s preview period. After this time, an auditory go-signal was presented, and shutter glasses remained open for another 3 seconds for participants to perform the posting or matching trial. The second group of participants performed the exact same task with the only difference that we introduced a 1-second delay between the end of the preview period and the presentation of the auditory go-signal. That is, shutter glasses closed after 1 second of preview during which participants were instructed to memorise the slot's orientation. After shutter glasses closed, participants had to wait with their matching/ posting movements until the go-signal was presented. In response to this signal, they performed their matching or posting movements without visibility of the posting apparatus and the moving limb (i.e., visually open-loop). Data was processed in the same way as in Experiments 1 and 2.
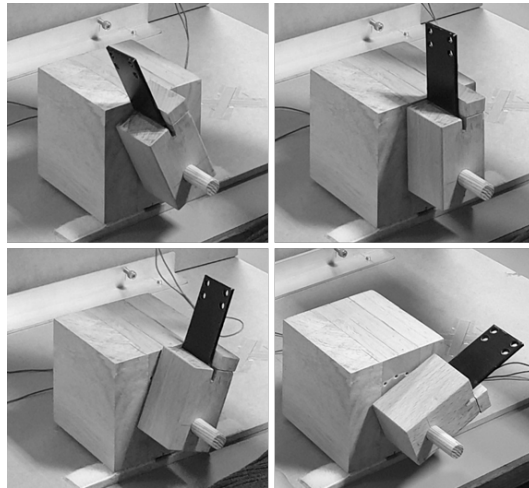
Figure 5: Start block used to place and rest the card prior to the movements in Experiment 3. For all slot orientations, the card needed to be rotated by 22.5° in clockwise direction to post or match the orientation of the slot. When placing the card at the 67.5° start orientation, the card was rested on the wooden block whereas for all other orientations it was rested on the black metal protrusion. This ensured that the card was centrally aligned to the slot for all start orientations.

Results

The first aim of this experiment was to test if, with constant rotation requirements for all slot orientations, the rotation dependent directional errors in card orientation are attenuated in posting (as compared to Experiments 1 and 2). We expected little effect of the rotation requirements on the directional errors in the matching task and thus expected them to remain similar to those observed in Experiments 1 and 2.

The directional errors for all slot orientations and both vision conditions in the matching task are depicted in Figures 6C. A descriptive comparison of the directional errors in the *matching tasks* of Experiments 1 (varying rotation requirements, Figure 2C) and 3 (constant rotation requirements, Figure 4C) shows that directional errors are very similar in both experiments. This was also confirmed statistically with a mixed ANOVA revealing no main effect of Experiment on directional errors in matching (all $p>.80$, $\eta_p^2<.002$) as well as no interaction effects between Experiment and slot orientation (all $p>.22$, $\eta_p^2<0.04$) in both vision and no-vision tasks. This confirms that directional errors in matching are, as expected, unaffected by the amount of rotation required.

Regarding the posting task, Figure 6D suggests that even though directional errors were substantially reduced as compared to Experiments 1 and 2 (Figures 2D and 4D), they still seemed to vary for the different slot orientations. In particular, even with similar rotation

requirements for all slot orientations, participants seemed to show a counterclockwise error for the horizontal (90°) slot orientation as compared to all other slot orientations. Statistical analysis confirmed that directional errors were significantly reduced in Experiment 3, where rotation requirements were kept consistent as compared to Experiment 1 where rotation requirements varied for the different slot orientations (main effect of experiment: full-vision condition, $F(1,34)=5.01$, $p=.03$, $\eta_p^2=0.13$, vs. no-vision conditions, $F(1,36)=48.29$, $p<.001$, $\eta_p^2=0.57$).

We assume that this persistent counterclockwise error for horizontal posting orientations can be attributed to the biomechanical demands of the posting task. Even though we matched the amount of rotation for all slot orientations, we were unable to ensure identical comfort across all slot orientations. Incidentally, our participants frequently reported that holding the card in the 67.5° start orientation (and posting horizontally) was the most uncomfortable. In other words, despite matching the rotation requirements for all conditions, we were unable to do the same for the comfort of the movement. As posting the card horizontally requires rotating the hand very close to the biomechanical limit, this may explain why movements were still biased counterclockwise in this condition.

The experiment's second aim was to determine if the oblique effect occurs in posting when rotation demands are similar for all slot orientations and, even more importantly, if the oblique effect is found in posting when a memory delay is introduced (as indicated by the absolute errors). This latter comparison allows us to distinguish between the predictions of the *processing* and *strategy hypotheses*.

Figure 6A shows that absolute errors in the *matching task* very closely resembled the pattern of results found for visually closed-loop and visually open-loop matching in Experiment 1 (Figure 2A). Unsurprisingly, matching errors were again larger when visual information was unavailable (delay condition). Furthermore, absolute orientation errors in both vision conditions showed again a clear oblique effect with consistently smaller errors for cardinal than for oblique slot orientations. As in Experiment 1, orientation errors were similar for the 22.5° and 45° degree slot orientations when full vision was available ($p=1$) but were larger for 22.5° as compared to the 45° (diagonal) slot orientation without visual information present ($p<.001$). These observations were confirmed by a 4 (slot orientation) x 2 (delay) mixed ANOVA on the absolute errors in the matching task revealing a main effect of slot orientation, $F(3,96)=26.92$, $p<.001$, $\eta_p^2=0.46$, a main effect of delay, $F(1,32)=37.38$, $p<.001$, $\eta_p^2=0.54$, and a significant interaction between the two factors, $F(3,96)=4.78$, $p=.005$, $\eta_p^2=0.13$. Thus, absolute errors in

the matching task were still determined by the slot orientation, even when the different target-orientations were associated with identical rotation demands. This confirms that absolute errors in matching are determined by perceptual and not by biomechanical factors.
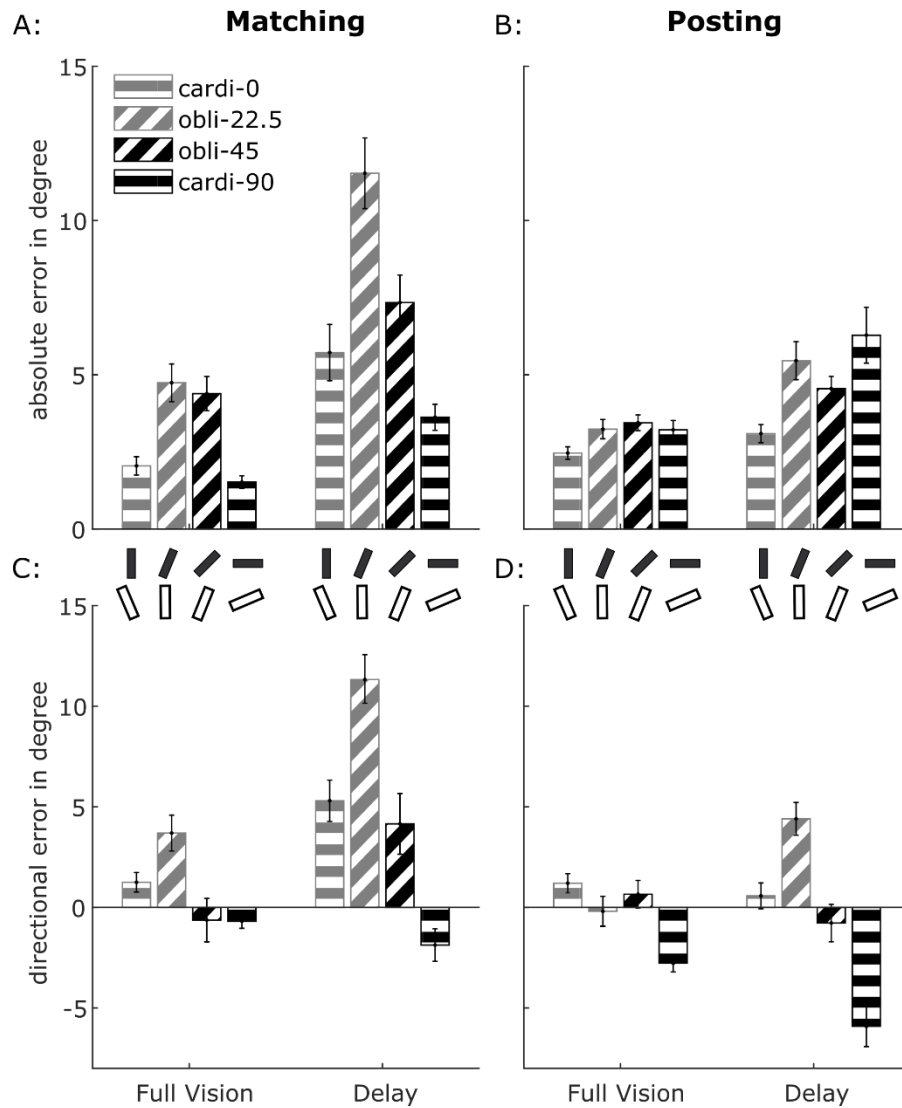

Figure 6: Absolute orientation errors (A and B) and directional orientation errors (C and D) as a function of slot orientation (indicated by black bar insets) and delay (full vision vs. 1-s Delay) in matching (A and C) and posting (B and D). The white bars below the black ones indicate the start orientation of the card. In the perceptual matching task absolute errors are consistent with an oblique effect (A) and directional errors (C) similar to Experiments 1 and 2. In contrast, even though rotation requirements were similar for all slot orientations as indicated by reduced directional errors in posting (D), an oblique effect emerged neither in the full vision nor in the delay condition (B). Positive values indicate clockwise and negative values counterclockwise directional errors. Both tasks were conducted visually closed-loop. Error bars indicate ±1 SEM (between subjects).

Regarding, the absolute errors in the *posting task*, Figure 6B suggests that by equating the amount of required rotation for all movements, absolute orientation errors became overall more similar for all slot orientations in the full-vision condition but still with no clear oblique effect arising. The same (i.e., the absence of a clear oblique effect) was true for the delay condition. This was confirmed by a 4 (slot orientation) x 2 (delay) mixed ANOVA on the absolute errors in the posting task. As expected, this analysis showed a significant main effect of delay with overall larger posting errors in the delay condition as compared to the full vision condition, $F(3,32)=25.78$, $p<.001$, $\eta_p^2=0.45$, as well as a main effect of slot orientation, $F(3,96)=6.16$, $p=.003$, $\eta_p^2=0.16$. However, there was no interaction between the factors ($p=.082$, $\eta_p^2=0.07$). Thus, orientation errors for the different slot orientations showed a similar pattern in both vision conditions. Post-hoc tests indicated that posting errors were significantly smaller for the vertical slot orientation as compared to all other orientations (all $p<.001$) for which the absolute errors did not differ from each other (all $p>.18$). The finding that absolute orientation errors for the different slot orientations in delayed posting did not differ from those in immediate posting (i.e., did not show an oblique effect) contradicts the predictions of the *processing hypothesis* (see Table 1).

Furthermore, the *processing hypothesis* predicts that errors in delayed posting should be similar to those in the matching conditions. To test this prediction, we conducted another 2 (task: matching vs. posting) x 4 (slot orientation) repeated-measures ANOVA on the absolute errors in the delay condition. This analysis revealed a significant interaction effect, $F(3,51)=12.70$, $p<.001$, $\eta_p^2=0.43$, confirming that absolute errors for the different slot orientations differ between matching and posting after delay. The fact that the pattern of absolute orientation errors for the different slot orientations remains different for posting and matching even when a delay is introduced is consistent with the predictions of the *strategy hypothesis*.

In summary, equating rotation demands had substantial effects on directional errors in the posting task but not in the matching task, suggesting that for matching, participants' priority is to achieve high accuracy independent of biomechanical demands. Furthermore, our findings are inconsistent with the prediction that absolute errors in posting after delay are equivalent to those made in a perceptual matching task. Therefore, it seems unlikely that the absence of an oblique effect in posting can be attributed to differences in visual orientation information processing in the perceptual versus the visuomotor systems. Instead, our findings highlight that posting and matching rely on different strategies, different sensory input and that in the

visuomotor tasks biomechanical demands, as well as the comfort and efficiency of movements, are highly relevant while those factors play no major role in the perceptual task.

General Discussion

The study aimed to assess if two tasks commonly used in neuropsychological assessments to determine deficits perceptual and visuomotor performance, both rely on visual orientation processing as previously assumed (Goodale & Milner, 2004; Goodale et al., 1991; Perenin & Vighetto, 1988). To do so, we measured the oblique effect, a well-known perceptual bias affecting human orientation perception, in a perceptual matching and a visuomotor letter-posting task. Across three different experiments, we found consistently larger absolute orientation errors in perceptual matching for oblique than cardinal orientations confirming the existence of a robust oblique effect in perception. In contrast, during visuomotor posting, error patterns did not follow an oblique effect but instead seemed to be primarily determined by the task's biomechanical demands. Specifically, in Experiment 1, we found directional errors towards the hand's start orientation consistent with the suggestions that biomechanical effort is reduced (and comfort increased) in an action task (Rosenbaum & Gaydos, 2008; Rosenbaum, Meulenbroek, Vaughan, & Jansen, 2001; Ross et al., 2014; Sparrow & Newell, 1998; Todorov, 2004). We tested this idea explicitly in Experiment 2 where we varied the start orientation of the hand and confirmed that directional posting errors were biased by the hand's start orientation while this was not observed during perceptual matching. Finally, in Experiment 3, we aimed to test if an oblique effect in posting may be revealed when rotation requirements, and thus biomechanical effort, are similar for all posting orientations in the action task. Both directional and absolute errors were attenuated in posting when we kept rotation requirements constant. However, contrary to perceptual matching, error patterns were not consistent with an oblique effect.

As outlined in the introduction, the absence of an oblique effect in visually-guided (Experiments 2 and 3) and visually open-loop (Experiment 1) posting is consistent with two different explanatory accounts. Firstly, it may indicate that visual orientation information is processed differently for perception and action, thus providing support for the *processing hypothesis* (Goodale et al., 1991; Milner & Goodale, 1995, 2006). Alternatively, it may indicate that posting does not require orientation processing at all but instead relies on different visual cues, thus providing support for the *strategy hypothesis* (Hesse et al., 2011). To differentiate between the two accounts, we tested matching and posting in a memory-guided condition

(Experiment 3). According to the *processing hypothesis*, the introduction of a short delay between visual presentation and movement initiation requires visual memory and would thus shift information processing for visuomotor guidance from the dorsal (visuomotor) to the ventral (perceptual) system (Goodale et al., 2005; Milner et al., 2003; Westwood & Goodale, 2003). Indeed a number of previous studies have found that perceptual biases that are not found in immediate action tasks, appear when a delay is introduced in this task and have interpreted this as support that delayed actions are guided by ventral stream information (e.g., Ganel et al., 2008; Singhal et al., 2007; Westwood & Goodale, 2003).

Thus, according to this assumption, posting after delay should rely on the same perceptual information as matching, and hence show the same error pattern (i.e., an oblique effect) as matching. Yet, our findings revealed that error patterns for matching and posting remained different even when introducing a delay with no oblique effect present in delayed posting. Furthermore, error patterns for the different slot orientations remained similar in immediate and delayed posting. These results support the idea that posting does not rely on visual orientation processing as predicted by the *strategy hypothesis*. The *strategy hypothesis* suggests that posting constitutes an obstacle avoidance task, where humans aim to clear the edges of the card from the edges of the posting slot without the need of explicitly processing visual orientation information (Hesse et al., 2011). Our conclusion is also in line with the presumed physiological origin of the oblique effect. Li, Peterson, and Freeman (2003), employing single-cell recordings in the cat brain, found that orientation-selective cells with a preference for horizontal and vertical angles are more prevalent in V1 than cells with a preference for oblique angles. On the basis of these findings it seems likely that the oblique effect is already present in V1. As V1 is assumed as the common origin of both dorsal and visual streams (Milner & Goodale, 1995; Ungerleider, Mishkin, Ingle, Goodale, & Mansfield, 1982), one may expect that this bias affects both ventral and dorsal visual representations. Consequently, regardless of whether visual information for a task is processed in the dorsal or ventral streams, performance may show an oblique effect as long as the task relies on visual orientation information. Thus, the presence of the oblique effect in matching and its absence in posting further supports the notion that matching uses orientation information while posting does not.

If posting does not rely on visual orientation processing as previously assumed, the question arises what skill or visual attribute do we measure in the posting task and what can we learn from previous neurological dissociations observed between those two tasks? To briefly recapitulate, the combination of perceptual matching and visuomotor posting has been

frequently used in the neuropsychological assessment of patients with perceptual or visuomotor deficits. In particular, in their seminal studies on patients suffering from optic ataxia, Perenin and Vighetto (1988) used this pair of tasks to show that these patients show specific impairments in using visual orientation information for action guidance despite showing normal perceptual performance in an orientation matching task. In the same vein, the two tasks were later used to assess the performance of patient DF, a well-known and extensively studied case of visual form agnosia (Goodale et al., 1991; Milner et al., 1991). The finding that DF and patients with optic ataxia seemed to show opposite patterns of behaviour - with normal visuomotor posting performance and strongly impaired perceptual matching performance in DF and the reverse pattern in optic ataxia - was interpreted in support of the idea of segregated functional systems processing vision for perception and vision for action (Goodale & Milner, 2004; but see Hesse, Ball, & Schenk, 2014 for an argument that this dissociation is not as clear as often described). However, the validity of such arguments depends on the assumption that both tasks rely on the same visual attribute; that is, visual orientation information.

If, however, as we concluded, posting does not rely on visual orientation information, how can we explain patients' selective problems with either matching or posting? If posting is indeed performed as an obstacle avoidance task, then success in this task relies on estimating egocentric distances (between the card/hand and the edge of the posting slot). The resulting notion that optic ataxia patients (but not DF) have specific problems with egocentric information processing is in line with findings from several previous studies (Buxbaum & Coslett, 1997; Carey, Dijkerman, Murphy, Goodale, & Milner, 2006; Schenk, 2006). Furthermore, the egocentric-deficit account is consistent with the general assumption that egocentric information processing relies on the dorsal system whereas allocentric information processing has been associated with the ventral system (e.g., Neggers, Van der Lubbe, Ramsey, & Postma, 2006; Zaehle et al., 2007). In addition, studies that look at obstacle avoidance tasks during reaching have found a similar pattern of results with retained obstacle avoidance after ventral stream damage (Rice et al., 2006) and impaired avoidance performance after dorsal stream damage (Schindler et al., 2004). In other words, while our findings suggest that based on dissociated performance in matching and posting, we cannot reliably establish the existence of segregated systems dealing with vision for perception and vision for action, the performance differences may more validly be related to specific issues in the processing of egocentric (distance) information that is required for posting but not for matching. It is worth noting, that we do not suggest that posting uses an egocentric version of orientation, instead we are saying

that posting remains unaffected by the oblique effect because it is performed without explicit use of visual orientation information.

Interestingly, a recent study suggests that the oblique effect may be shaped by both allocentric *and* egocentric cues. Mikellidou et al. (2015) examined the effect of head-tilt on the oblique effect and found that head-tilt has little effect when observers are sitting upright but leads to a substantial change in the oblique bias when observers are lying on their back. When combined with our findings of the oblique effect affecting only the perceptual matching task but not the visuomotor posting task, an interesting conclusion emerges: a bias shaped significantly by egocentric information can have a selective effect on perceptual judgments. This illustrates that the presumed mapping of allocentric coding onto perception and egocentric coding onto action may also be too simple and not capture the true richness of sensory integration needed for both perception and action.

More generally, our findings highlight the issues associated with matching perceptual and visuomotor tasks and making conclusions based on the resulting error patterns. In many previous studies, dissociations in biases and error patterns between perceptual and visuomotor tasks have been interpreted in support of distinct representations and processing areas (e.g., Aglioti et al., 1995; Ganel et al., 2008; Ganel & Goodale, 2003; Haffenden & Goodale, 1998). Yet, more recently, an increasing number of studies seems to conclude that alternative factors, such as biomechanical task differences, differences in task strategies and/or the use of visual cues can explain the observed dissociations more parsimoniously (e.g., Franz & Gegenfurtner, 2008; Mon-Williams & Bull, 2000; Ross et al., 2014; Schenk, 2006; Schenk, Utz, & Hesse, 2017; Smeets & Brenner, 2008; Smeets, Brenner, de Grave, & Cuijpers, 2002; Utz, Hesse, Aschenneller, & Schenk, 2015; Vishton, Pea, Cutting, & Nunez, 1999).

<u>Acknowledgment</u>

References

Aglioti, S., DeSouza, J. F. X., & Goodale, M. A. (1995). Size-contrast illusions deceive the eye but not the hand. *Current Biology, 5*(6), 679-685.

Appelle, S., & Gravetter, F. (1985). Effect of modality-specific experience on visual and haptic judgment of orientation. *Perception, 14*(6), 763-773.

Buxbaum, L. J., & Coslett, H. B. (1997). Subtypes of optic ataxia: Reframing the disconnection account. *Neurocase, 3*(3), 159-166.

Campbell, F. W., Kulikowski, J. J., & Levinson, J. (1966). The effect of orientation on the visual resolution of gratings. *The Journal of Physiology, 187*(2), 427-436.

Carey, D. P., Dijkerman, H. C., Murphy, K. J., Goodale, M. A., & Milner, A. D. (2006). Pointing to places and spaces in a patient with visual form agnosia. *Neuropsychologia, 44*(9), 1584-1594.

Cohen, R. G., Biddle, J. C., & Rosenbaum, D. A. (2010). Manual obstacle avoidance takes into account visual uncertainty, motor noise, and biomechanical costs. *Experimental Brain Research, 201*(3), 587-592.

Corwin, T. R., Moskowitz-Cook, A., & Green, M. A. (1977). The oblique effect in a vernier acuity situation. *Perception & Psychophysics, 21*(5), 445-449.

Cos, I., Bélanger, N., & Cisek, P. (2011). The influence of predicted arm biomechanics on decision-making. *Journal of Neurophysiology, 105*, 3022-3033.

Cos, I., Medleg, F., & Cisek, P. (2012). The modulatory influence of endpoint controllability on decisions between actions. *Journal of Neurophysiology, 108*, 1764-1780.

Cuijpers, R. H., Kappers, A. M., & Koenderink, J. J. (2000). Large systematic deviations in visual parallelism. *Perception, 29*(12), 1467-1482.

Franz, V. H. (2004). The Optotrak Toolbox.

Franz, V. H., & Gegenfurtner, K. (2008). Grasping visual illusions: Consistent data and no dissociation. *Cognitive Neuropsychology, 25*(7-8), 920-950. doi:10.1080/02643290701862449

Franz, V. H., Hesse, C., & Kollath, S. (2009). Visual illusions, delayed grasping, and memory: No shift from dorsal to ventral control. *Neuropsychologia, 47*(6), 1518-1531. doi:10.1016/j.neuropsychologia.2008.08.029

Ganel, T., Chajut, E., & Algom, D. (2008). Visual coding for action violates fundamental psychophysical principles. *Current Biology, 18*(14), R599-R601.

Ganel, T., & Goodale, M. A. (2003). Visual control of action but not perception requires analytical processing of object shape. *Nature, 426*, 664-667.

Goodale, M. A., Kroliczak, G., & Westwood, D. A. (2005). Dual routes to action: Contributions of the dorsal and ventral streams to adaptive behavior. *Progress in Brain Research, 149*, 269-283.

Goodale, M. A., & Milner, A. D. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences, 15*, 97-112.

Goodale, M. A., & Milner, A. D. (2004). *Sight Unseen: An Exploration of Conscious and Unconscious Vision*: Oxford: Oxford University Press.

Goodale, M. A., Milner, A. D., Jakobson, L. S., & Carey, D. P. (1991). A neurological dissociation between perceiving objects and grasping them. *Nature, 349*, 154-156.

Goodale, M. A., Westwood, D. A., & Milner, A. D. (2004). Two distinct modes of control for object-directed action. *Progress in Brain Research, 144*, 131-144.

Gosselin-Kessiby, N., Messier, J., & Kalaska, J. F. (2008). Evidence for automatic on--line adjustments of hand orientation during natural reaching movements to stationary targets. *Journal of Neurophysiology, 99*, 1653-1671.

Greenhouse, S. W., & Geisser, S. (1959). On methods in the analysis of profile data. *Psychometrika, 24*(2), 95-112.

Haaxma, R., & Kuypers, H. G. J. M. (1974). Role of occipito-frontal cortico-cortical connections in visual guidance of relatively independent hand and finger movements in rhesus monkeys. *Brain Research, 71*(2-3), 361-366.

Haaxma, R., & Kuypers, H. G. J. M. (1975). Intrahemispheric cortical connections and visaul guidance of hand and finger movements in the rhesus monkey. *Brain, 97*, 239-260.

Haffenden, A. M., & Goodale, M. A. (1998). The effect of pictorial illusion on prehension and perception. *Journal of Cognitive Neuroscience, 10*(1), 122-136.

Hermens, F., & Gielen, S. (2003). Visual and haptic matching of perceived orientations of lines. *Perception, 32*(2), 235-248.

Hesse, C., Ball, K., & Schenk, T. (2014). Pointing in visual periphery: is DF's dorsal stream intact? *Plos One, 9*(3), e91420.

Hesse, C., & Deubel, H. (2009). Changes in grasping kinematics due to different start postures of the hand. *Human Movement Science, 28*(4), 415-436. doi:10.1016/j.humov.2009.03.001

Hesse, C., Franz, V. H., & Schenk, T. (2011). Letter Posting and Orientation Matching: Two Equivalent Tasks in Action and Perception? *Seeing and Perceiving, 24*(2), 151-172. doi:10.1163/187847511x570105

Hesse, C., Kangur, K., & Hunt, A. R. (2020). Decision making in slow and rapid reaching: Sacrificing success to minimize effort. *Cognition, 205*, 104426.

Hesse, C., & Schenk, T. (2014). Delayed action does not always require the ventral stream: a study on a patient with visual form agnosia. *Cortex, 54*, 77-91.

Ishihara, S. (1917). *Tests for colour blindness*. Tokyo, Japan: Hongo Harukicho.

James, T. W., Culham, J., Humphrey, G. K., Milner, A. D., & Goodale, M. A. (2003). Ventral occipital lesions impair object recognition but not object-directed grasping: an fMRI study. *Brain, 126*, 2463-2475.

Jeannerod, M. (1988). *The neural and behavioral organization of goal--directed movements*: Oxford: Oxford University Press.

Jeannerod, M., Long, J., & Baddeley, A. (1981). Intersegmental coordination during reaching at natural visual objects. In *Attention and Performance* (Vol. 9, pp. 153-168): Hillsdale, NJ: Erlbaum.

Julesz, B. (1971). *Foundations of cyclopean perception*. Chicago: University of Chicago Press.

Kappers, A. M., & Koenderink, J. J. (1999). Haptic perception of spatial relations. *Perception, 28*(6), 781-795.

Kleinholdermann, U., Franz, V. H., & Gegenfurtner, K. R. (2013). Human grasp point selection. *Journal of Vision, 13*(8), 1-12.

Kopiske, K. K., Bruno, N., Hesse, C., Schenk, T., & Franz, V. H. (2016). The functional subdivision of the visual brain: Is there a real illusion effect on action? A multi-lab replication study. *Cortex, 79*, 130-152.

Lechelt, E. C., & Verenka, A. (1980). Spatial anisotropy in intramodal and cross-modal judgments of stimulus orientation: The stability of the oblique effect. *Perception, 9*(5), 581-589.

Lederman, S. J., & Wing, A. M. (2003). Perceptual judgement, grasp point selection and object symmetry. *Experimental Brain Research, 152*(2), 156-165.

Li, B., Peterson, M. R., & Freeman, R. D. (2003). Oblique effect: a neural basis in the visual cortex. *Journal of Neurophysiology, 90*(1), 204-217.

Lommertzen, J., E Silva, E. C., Cuijpers, R. H., & Meulenbroek, R. G. (2009). Collision-Avoidance Characteristics of Grasping. In G. Pezzulo, M. V. Butz, O. Sigaud, & G. Baldassarre (Eds.), *Anticipatory Behavior in Adaptive Learning Systems: From Psychological Theories to Artificial Cognitive Systems* (Vol. 5499, pp. 188-208). Berlin Heidelberg: Springer.

Mikellidou, K., Cicchini, G. M., Thompson, P. G., & Burr, D. C. (2015). The oblique effect is both allocentric and egocentric. *Journal of Vision, 15*(8), 24.

Milgram, P. (1987). A spectacle-mounted liquid-crystal tachistoscope. *Behavior Research Methods, Instruments, & Computers, 19*(5), 449-456.

Milner, A. D., Dijkerman, H. C., McIntosh, R. D., Rossetti, Y., & Pisella, L. (2003). Delayed reaching and grasping in patients with optic ataxia. *Progress in Brain Research, 142*, 225-242.

Milner, A. D., & Goodale, M. A. (1995). *The visual brain in action*: Oxford: Oxford University Press.

Milner, A. D., & Goodale, M. A. (2006). *The visual brain in action.* (2nd ed.). Oxford: Oxford University Press.

Milner, A. D., Perrett, D. I., Johnston, R. S., Benson, P. J., Jordan, T. R., Heeley, D. W., . . . Terazzi, E. (1991). Perception and action in visual form agnosia. *Brain, 114*, 405-428.

Mon-Williams, M., & Bull, R. (2000). The Judd illusion: Evidence for two visual streams or two experimental conditions? *Experimental Brain Research, 130*, 273-276.

Neggers, S. F., Van der Lubbe, R. H., Ramsey, N. F., & Postma, A. (2006). Interactions between ego-and allocentric neuronal representations of space. *Neuroimage, 31*(1), 320-331.

Perenin, M. T., & Vighetto, A. (1988). Optic ataxia: A specific disruption in visuomotor mechanisms. I. Different aspects of the deficit in reaching for objects. *Brain, 111*, 643-674.

Rice, N. J., McIntosh, R. D., Schindler, I., Mon-Williams, M., Démonet, J. F., & Milner, D. A. (2006). Intact automatic avoidance of obstacles in patients with visual form agnosia. *Experimental Brain Research, 174*, 176-188.

Rosenbaum, D. A., & Gaydos, M. J. (2008). A method for obtaining psychophysical estimates of movement costs. *Journal of Motor Behavior, 40*(1), 11-17.

Rosenbaum, D. A., & Gregory, R. W. (2002). Development of a method for measuring movement-related effort. *Experimental Brain Research, 142*(3), 365-373.

Rosenbaum, D. A., Meulenbroek, R. G., Vaughan, J., & Jansen, C. (1999). Coordination of reaching and grasping by capitalizing on obstacle avoidance and other constraints. *Experimental Brain Research, 128*(1-2), 92-100.

Rosenbaum, D. A., Meulenbroek, R. J., Vaughan, J., & Jansen, C. (2001). Posture-based motion planning: applications to grasping. *Psychological Review, 108*(4), 709-734.

Ross, A. I., Schenk, T., & Hesse, C. (2014). Line-bisectioning and obstacle avoidance: Evidence for separate strategies. *Acta Psychologica, 151*, 74-82.

Schenk, T. (2006). An allocentric rather than perceptual deficit in patient DF. *Nature Neuroscience, 9*, 1369-1370.

Schenk, T., Utz, K. S., & Hesse, C. (2017). Violations of Weber's law tell us more about methodological challenges in sensorimotor research than about the neural correlates of visual behaviour. *Vision Research, 140*, 140-143.

Schindler, I., Rice, N. J., McIntosh, R. D., Rossetti, Y., Vighetto, A., & Milner, A. D. (2004). Automatic avoidance of obstacles is a dorsal stream function: Evidence from optic ataxia. *Nature Neuroscience, 7*, 779-784.

Singhal, A., Culham, J. C., Chinellato, E., & Goodale, M. A. (2007). Dual-task interference is greater in delayed grasping than in visually guided grasping. *Journal of Vision, 7*(5), 5-5.

Smeets, J. B. J., & Brenner, E. (2008). Grasping Weber's law. *Current Biology, 18*(23), 1089-1090.

Smeets, J. B. J., Brenner, E., de Grave, D. D. J., & Cuijpers, R. H. (2002). Illusions in action: Consequences of inconsistent processing of spatial attributes. *Experimental Brain Research, 147*, 135-144.

Snellen, H. (1862). *Probebuchstaben zur Bestimmung der Sehschärfe*. Utrecht, The Netherlands: van de Weijer, P. W.

Soechting, J. F., & Flanders, M. (1993). Parallel, interdependent channels for location and orientation in sensorimotor transformations for reaching and grasping. *Journal of Neurophysiology, 70*(3), 1137-1150.

Sparrow, W. A., & Newell, K. M. (1998). Metabolic energy expenditure and the regulation of movement economy. *Psychonomic Bulletin & Review, 5*(2), 173-196.

Todorov, E. (2004). Optimality principles in sensorimotor control. *Nature Neuroscience, 7*(9), 907-915.

Ungerleider, L. G., Mishkin, M., Ingle, D. J., Goodale, M. A., & Mansfield, R. J. W. (1982). Two cortical visual systems. In *Analysis of visual behavior* (pp. 549-586): Cambridge, MA: MIT Press.

Utz, K. S., Hesse, C., Aschenneller, N., & Schenk, T. (2015). Biomechanical factors may explain why grasping violates Weber's law. *Vision Research, 111*, 22-30.

Utz, K. S., Hesse, C., Hintz, A., Grüneberger, D., Kulke, H., Roth, I., . . . Schenk, T. (2018). Visual feedback explains why propointing is better than antipointing in spatial neglect. *Cortex, 98*, 114-127.

Vishton, P. M., Pea, J. G., Cutting, J. E., & Nunez, L. N. (1999). Comparing effects of the horizontal-vertical illusion on grip scaling and judgment: Relative versus absolute, not perception versus action. *Journal of Experimental Psychology: Human Perception and Performance, 25*, 1659-1672.

Vogels, R., & Orban, G. A. (1985). The effect of practice on the oblique effect in line orientation judgments. *Vision Research, 25*(11), 1679-1687.

Westwood, D. A., & Goodale, M. A. (2003). Perceptual illusion and the real-time control of action. *Spatial Vision, 16*(3-4), 243-254.

Westwood, D. A., Heath, M., & Roy, E. A. (2003). No evidence for accurate visuomotor memory: systematic and variable error in memory-guided reaching. *Journal of Motor Behavior, 35*(2), 127-133.

Westwood, D. A., McEachern, T., & Roy, E. A. (2001). Delayed grasping of a Mueller-Lyer figure. *Experimental Brain Research, 141*, 166-173.

Zaehle, T., Jordan, K., Wüstenberg, T., Baudewig, J., Dechent, P., & Mast, F. W. (2007). The neural basis of the egocentric and allocentric spatial frame of reference. *Brain Research, 1137*, 92-103.