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Immediate and delayed actions share a common visuomotor transformation mechanism: A prism adaptation study

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ABSTRACT

It is a key assumption of the perception/action model that the dorsal stream relies on current visual input and does not store visual information over an extended period of time. Consequently, it is expected that action which is guided by memorized visual information, so-called *delayed action*, cannot use information from the dorsal stream but must rely instead on the ventral stream input. However, it is currently unclear how the information from the ventral stream can be used to guide an action. This issue is particularly challenging given that the perception/action model also assumes that ventral stream input is not particularly useful for guiding actions since the information it provides is coded relative to the visual scene and not relative to the observer. We describe two possible solutions to this problem and suggest that they can be tested using the prism adaptation paradigm. Subjects in our study were adapted to optical prisms using either an immediate or a delayed pointing task. In both cases, subjects showed the typical post-exposure negative aftereffect. Moreover, there was almost complete transfer of the aftereffect between immediate and delayed pointing. This is particularly surprising given the long history of findings showing little transfer between motor tasks for which separate neural representations are assumed. In this context our findings suggest a substantial overlap in the visuomotor transformation processes used for immediate and delayed pointing.

1. Introduction

Ungerleider and Mishkin (1982; U&M) proposed that the visual brain comprises two separate cortical pathways: a dorsal stream, projecting from primary visual cortex (PVC) to the posterior parietal cortex (PPC) that processes spatial information, and a ventral stream, projecting from PVC to inferior temporal cortex (ITC) that is concerned with information about the properties of objects. This hypothesis was based on observations from primate lesion studies in which damage to the monkey PPC disrupted the ability to 'select' objects based on their proximity to a visual landmark, while leaving intact the ability to 'recognise' objects. In contrast, monkeys with damage to the ITC were able to perceive the spatial relations among objects but could not discriminate between the objects themselves. Accordingly, the ventral stream was described as a 'what' system that is specialised for identifying objects (i.e. object perception), and the dorsal stream as a 'where' system that is critical for locating the position of an object (i.e. spatial perception); the assumption being that together the two streams provide to a single representation of the visual environment.

More recently, Milner and Goodale (1995; M&G) have argued that the 'what versus where' model fails to capture the essential difference between the *functions* of the two streams. In contrast to U&M's emphasis on the parallel processing of *incoming* information about different visual attributes, M&G's (1995) perception/action model focuses instead on the different *output* requirements of the streams. Indeed, they propose that *both* cortical streams process information about the intrinsic properties of objects (e.g. size, shape, and orientation) and their location, but that the transformations they carry out are matched to the distinct purposes for which each stream has evolved: the dorsal stream for the control of visually guided action and the ventral stream for the perception and recognition of objects.

Evidence to support this functional distinction comes primarily from studies of patients with a lesion to only one of the two cortical streams. In particular, the opposite pattern of impairment and preserved ability in patients with 'visual form agnosia' (VFA) and 'optic ataxia' (OA) is suggested to demonstrate a double dissociation between vision for action and vision for perception. Patient DF, for example, who has VFA as a result of extensive bilateral damage to the lateral occipital complex in the ventral stream, is unable to identify familiar objects or estimate their size,

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shape or orientation, yet she can still reach out and accurately scale the opening of her hand to grasp these objects. According to M&G (1995), this preserved motor skill can be attributed to DF's largely intact dorsal stream. In contrast, OA patient IG, who has severe bilateral damage to the PPC, has no difficulty indicating the properties of objects, but she is unable to accurately scale her grip size when reaching for them (Milner et al., 2001).

Another key assumption of the perception/action model is that the two visual streams operate under different temporal constraints and frames of reference. M&G (1995) suggest that in order to meet the requirements of a goal-directed task, the 'action' system provides a constantly updated visual representation of a target object in coordinates relative to the observer (i.e. within an egocentric frame of reference) so that, even if the observer moves around the environment, the visual input remains both relevant and accurate for specifying the action. Consequently, the dorsal stream is proposed to use "just-in-time computations" to transform retinal input "at the moment the movement is about to be performed" (M&G, 2006, p. 247). In contrast, the ventral stream is suggested to retain visual information over a much longer time scale and within an allocentric (i.e. scene-based) frame of reference, so that objects can be recognised many months, even years, later in different viewing conditions or contexts.

This temporal dissociation in the two streams is supported by a number of findings. In an early study, for example, when healthy subjects pointed to a visual target that had been occluded 2 s before movement onset, their pointing error doubled compared with an immediate pointing condition. This seems to indicate that the highly accurate representation provided by the dorsal stream is available for less than 2 s after visual information is withdrawn (Elliott & Madalena, 1987). A similar study suggests, however, that a switch is made to the less accurate perceptual representation less than 500 ms after a target is hidden from view (Westwood, Heath, & Roy, 2001). By far the strongest claim about the temporal differences of the two visual streams is made by Westwood and Goodale's (2003) 'real-time' hypothesis, which proposes that the dorsal stream representation plays no role at all in the control of memory-guided movements, but rather "the dedicated, real-time visuomotor mechanisms are engaged for the control of action only after the response is cued, and only if the target is visible" (p. 243). More recently, this view has been endorsed by M&G (2006).

However, the most striking evidence in support of the distinct temporal properties of the two visual streams comes from work with neurological patients. As mentioned earlier, VFA patient DF can grasp objects normally under immediate responding conditions. However, when her grasp is delayed by 2 s, her ability to accurately scale her anticipatory finger–thumb grip size is clearly abnormal (Goodale, Jakobson, & Keillor, 1994). Similarly, she is able to point as accurately as three control subjects when making an immediate response, but when a delay of 10 s is imposed between viewing the target and movement onset, her pointing error becomes twice as large as that of controls (Milner, Dijkerman, & Carey, 1999). In contrast, OA patient AT shows severe visuomotor impairment under immediate conditions yet, paradoxically, she is able to point both faster and more accurately when a 5 s delay is introduced between target occlusion and movement onset (Milner, Paulignan, Dijkerman, Michel, & Jeannerod, 1999). However, it should be noted that this evidence has been somewhat weakened since Himmelbach and Karnath (2005) re-examined the influence of delays on visuomotor performance in OA and found that, even after a delay, visuomotor performance in OA patients is still significantly worse than that of healthy subjects. Moreover, they observed a *gradual* increase of pointing accuracy as the delay duration increased rather than an abrupt switch in performance at a specific delay.

If we accept the concept of separate visual pathways for immediate and delayed action then we are faced with the question of how, in the case of delayed action, information from the ventral stream is used to guide action. This poses a particularly challenging problem given some of the other assumptions that underpin the perception/action model. As described earlier, according to the model, the ventral stream codes visuospatial information in an allocentric framework—an assumption that has been supported in a number of studies with the VFA patient DF (e.g. Carey, Dijkerman, Murphy, Goodale, & Milner, 2006; Carey, Harvey, & Milner, 1996; Schenk, 2006). However, it is also commonly accepted that for the visual guidance of goal-directed action, in particular for reaching movements, the target position is typically coded in an egocentric reference system which could be centred, for example, in the hand or shoulder (Flanders, Helms-Tillery, & Soechting, 1992; Vetter, Goodbody, & Wolpert, 1999). In the case of immediate action, the perception/action model assumes that the relevant visual information about the target is represented first in retinotopic coordinates and then transformed to hand/shoulder coordinates in the dorsal stream. However, we do not know how visual information is transformed to guide delayed action, since the visual input presumably originates in the ventral stream and is therefore represented in an allocentric code (cf. Westwood & Goodale, 2003).

One solution could be that the two types of actions use separate visuomotor transformation mechanisms, which rely on entirely different processes and distinct neural pathways. If this is the case, then one pathway, used for immediate action, would first translate retinotopic input into egocentric code and then into appropriate motor parameters, whereas a second pathway would allow the transformation of allocentrically coded target information into appropriate motor parameters for delayed action.

Alternatively, a common visuomotor transformation mechanism could be used for both delayed *and* immediate action. In this case, although delayed and immediate action may receive their visual input from different sources and in different formats (i.e. direct retinotopic input from the dorsal stream in the case of immediate action compared with indirect allocentric input from the ventral stream in the case of delayed action), in both cases the visual input would first be translated into a common egocentric format and then into appropriate motor parameters.

Here we suggest that the prism adaptation (PA) paradigm can be used to distinguish between the two different hypotheses. In the standard PA paradigm, subjects wear glasses with prism lenses that shift the visual scene laterally, for example to the right. Thus, when subjects initially point to a visual target they land to the right of it. With trial and error, subjects' pointing errors quickly decrease and they are again able to point accurately to the target. This error reduction reflects the process of *adaptation*. When the prism glasses are removed subjects initially produce pointing errors in the opposite direction to the prism displacement demonstrating a *negative aftereffect*.

PA is thought to involve two dissociable processes (Redding & Wallace, 1996). The first is a *strategic component* involving the use of conscious strategies to reduce pointing error during the adaptation phase, such as deliberate side-pointing and online movement–path corrections (Newport & Jackson, 2006). In addition, the motor command can also be updated with offline information from previous unsuccessful trials. The second component of PA is referred to as *spatial realignment*. To allow the successful visual guidance of arm and hand movements, it is important that *proprioceptive* information about the position of the arm and hand can be related to *visual* information about both the target and the arm and hand. This relies on a consistent relationship between visually- and proprioceptively perceived locations. Prism glasses affect only the visual information, resulting in the visuo-proprioceptive relationship being misaligned. However, during the adaptation process a new relationship develops which ensures that the seen and felt position of the hand and limb become re-aligned. This realignment involves a shift of the visual map relative to the proprioceptive map. In contrast to strategic control, spatial realignment is a non-conscious process, it takes longer to develop, and it is largely responsible for the negative aftereffects demonstrated when the prism glasses are removed following adaptation.

In short, PA induces a bias in the visuomotor transformation mechanism and this bias is reflected in the size of the negative aftereffect. Importantly, it has been demonstrated in many studies that even slight changes in the task characteristics (e.g. switching from an underhand to an overhand throw or switching between different movement speeds) can be enough to prevent the transfer of visuomotor adaptation between two tasks (Baraduc & Wolpert, 2002; Field, Shipley, & Cunningham, 1999; Kitzawa, Kimura, & Uka, 1997; Martin, Keating, Goodkin, Bastian, & Thach, 1996b). Commonly this has been interpreted as evidence that the different tasks use separate visuomotor mapping procedures (Baraduc & Wolpert, 2002). Conversely, shared visuomotor mapping procedures are assumed if substantial transfer between two tasks is observed. This provides us with an opportunity to test which of the two scenarios best describes the visuomotor transformation processes engaged in immediate and delayed action.

Little transfer of PA between immediate and delayed pointing is expected if we assume that the two types of actions use distinct visuomotor transformation pathways. Conversely, substantial transfer is expected if immediate and delayed pointing use the same visuomotor transformation mechanism.

In the present study we investigated the effects of PA on both immediate and delayed action. Most importantly, we measured whether PA using an immediate pointing task produced a substantial negative aftereffect for pointing under delayed conditions and whether PA using a delayed pointing task transferred to subsequent pointing under immediate conditions.

2. Method

We conducted two PA experiments. In both experiments, immediate and delayed pointing accuracy was tested in the baseline and post-adaptation phases. The two experiments differed only with respect to the adaptation phase: in Experiment 1 only immediate pointing was used during the adaptation phase, whereas only delayed pointing was used in Experiment 2.

2.1. Subjects

A total of 19 right-handed male subjects participated in the study (10 in Experiment 1 and 9 in Experiment 2). All had normal or corrected-to-normal vision and no history of neurological disorder. Subjects were naïve to the purpose of the study. The experiment was conducted in accordance with the 1964 Declaration of Helsinki and with the approval of the Ethics Committee of the Psychology Department at Durham University. All participants gave their informed verbal consent prior to testing.

2.2. Apparatus

The same setup was used in Experiments 1 and 2. This comprised a row of 4 green-LED targets, positioned at a distance of 40 cm from the observer (targets 1 and 2 were located 15 and 5 cm to the left of centre, respectively, and targets 3 and 4 were at equivalent distances to the right). The targets were covered with perspex to prevent tactile feedback about the target-LEDs. An electronic switch was used to indicate the start of the pointing movement. Subjects had to hold the switch down at the beginning of the trial and release it at the start of their pointing movement. Movements were recorded with a 3D movement registration system (CMS 70, Zebris, Isny, Germany; sampling frequency: 50 Hz; spatial resolution: 0.1 mm), which used a panel of microphones to detect ultrasonic signals given out by a single loudspeaker attached to the subject's right index finger. A pair of photo-sensors, which were positioned at a distance of 36 cm from the observer (i.e. 4 cm closer to the observer than the targets), were used to detect when the subject's hand came into the vicinity of the target-LEDs and to trigger the onset of the terminal visual feedback (see Section 2.3). All the devices were controlled by a PC which also produced a short tone at the beginning of each trial as a 'go' signal. During the adaptation phase subjects wore rightward-shifting wedge-shaped prism glasses of five different strengths (2°, 4°, 8°, 12°, and 15°).

2.3. Experimental procedure

2.3.1. Procedures common to both Experiment 1 and 2

Currently there are many different paradigms for prism adaptation in use. In the following we briefly describe and justify the paradigm we have adopted for our two experiments. As our main variable of interest was the size of the negative aftereffect, two factors known to induce large aftereffects were included in the PA procedure: *terminal error feedback* (i.e. sight of the pointing finger relative to the target at the end of the movement path only [Redding & Wallace, 1997]), and *gradual exposure* to the visual displacement using prisms of five increasing strengths (Kagerer, Contreras-Vidal, & Stelmach, 1997). Previous studies have shown that when the magnitude of the prism distortion is introduced at levels below a subject's awareness threshold, there is typically little or no use of strategic corrections but very pronounced prismatic aftereffects (e.g. Michel, Pisella, Prablanc, Rode, & Rossetti, 2007).

The aftereffects were assessed using a visual open-loop task (i.e. pointing to a target without sight of the hand), which provides a combined measure of visual and proprioceptive remapping (Redding & Wallace, 1992; Sarri et al., 2008). While we were interested in *visual* shift only, it is known that the visual system undergoes much greater remapping than the proprioceptive system when terminal visual feedback (as opposed to sight of the entire movement path) is available during the adaptation phase (Redding & Wallace, 1997, 2000). As terminal feedback was used in our experiment, the traditionally used open-loop pointing task was considered to be both a convenient and appropriate method for measuring the PA aftereffects.

2.3.2. Experiment 1

The experiment consisted of three phases: the pre-adaptation phase (i.e. pointing without prism glasses *prior* to the adaptation phase); adaptation phase (i.e. pointing with prism glasses); and post-adaptation phase (i.e. pointing without prism glasses *after* the adaptation phase). During the pre- and post-adaptation phases two different trial types were used, namely immediate pointing (type-1) and delayed pointing (type-2). No visual feedback about hand position was provided during these phases. In the adaptation phase all trials required an immediate pointing response (type-3) and terminal feedback about the hand position was provided.

During all trials subjects were seated at a table in a dark room. They were instructed to point with their right index finger to the target-LED. At the beginning of each trial subjects had their finger on the start button. A target-LED was then switched on. For the type-1 trials (immediate pointing/no feedback), a tone was emitted (mandatory go-signal) after 2 s to instruct subjects to initiate their movement. The target-LED was switched off as soon as the subject started their pointing movement (i.e. released the start-button). During the movement no visual information (neither about the target nor the hand) was provided. The only difference for the type-2 trials (delayed pointing/no feedback) was that the target-LED was switched off after 2 s and the mandatory go-signal (tone) was delayed by a further 3 s (i.e. subjects had to point to a remembered target). The rest of the trial proceeded in the same way as type-1 trials. Type-3 trials (immediate pointing/terminal feedback) were presented during the adaptation phase only. Again subjects began with their finger on the start-button, a target-LED was switched on, the go-signal tone was given after 2 s, and the target-LED was switched off as soon as subjects released the start-button. However, in contrast to type-1 and -2 trials, just before the subject reached the target their hand crossed the line between a pair of photosensors that activated the green target-LED and the red finger-LED, thereby providing terminal visual feedback. Both LEDs remained on for 500 ms.

The experiment began with the pre-adaptation phase which consisted of one block of 40 pointing trials (20 type-1 plus 20 type-2 trials) without visual feedback. The 4 target locations and 2 pointing conditions were presented in a randomized sequence. In the second phase (adaptation), 5 blocks were presented (4 blocks of 20 type-3 trials followed by 1 block of 40 type-3 trials). The strength of the prism glasses increased from block to block starting at 2° up to 15° (see Section 2.2 for details). The procedure for the final experimental phase (post-adaptation) was identical to that of the pre-adaptation phase.

2.3.3. Experiment 2

The procedure for Experiment 2 was identical to Experiment 1 except with respect to the type of pointing trial used in the adaptation phase. In Experiment 2 all trials required a *delayed* pointing response and terminal feedback about the hand position was provided (type-4). At the start of each trial subjects had their finger on the start button. A target-LED was then switched on. This went off after 2 s and the mandatory go-signal tone was delayed by a further 3 s (i.e. subjects had to point to a remembered target). Feedback was provided at the end of the movement. Shortly before subjects reached the target their hand blocked a photosensor. This then triggered the onset of the red-finger LED and the green target-LED. Both LEDs remained on for 500 ms. Given that the target-LED was switched on again at the end of the movement, one might argue that this procedure did not provide a pure delayed-pointing condition. However, the onset of the target information practically coincided with the end of the movement—in fact all subjects were convinced that the target and feedback LEDs were switched on *after* they had completed their movement. It is therefore unlikely that subjects could use this terminal target information to modify their response in that trial. We can therefore assume that they based their movements on the remembered target position and accordingly conclude that they used the delayed-pointing mode during the adaptation procedure of Experiment 2.

2.3.4. Data analysis

Our main outcome variable was the constant error (i.e. the mean distance between the endpoint of the finger and the position of the target). A negative error indicates a bias towards the left. Due to recording artefacts or gaps in the recording of the 3D movement registration system, 5% of trials had to be discarded. Within-subject *t*-tests and a significance threshold of 5% were used.

3. Results

3.1. Experiment 1—Effects of immediate PA on immediate and delayed pointing accuracy

We tested whether PA (using an immediate pointing task) induced a significant shift, by comparing the constant error for the pre- and post-adaptation phases. A significant and comparable shift was found both for the immediate ($t(9) = 8.807$, $p < 0.001$) and the delayed pointing tasks ($t(9) = 9.364$, $p < 0.001$). The induced shift in the two conditions was almost identical (see Fig. 1): in the immediate condition PA induced a shift of 78.06 mm (S.D. = 28.03), and in the delayed condition a shift of 77.98 mm (S.D. = 26.33) was induced. A paired *t*-test confirmed that the difference between the shift in the immediate and delayed conditions was not significant ($t(9) = -0.021$, $p = 0.984$). To test whether there was a significant relationship between the shift in the immediate and delayed pointing we carried out a correlational analysis (Pearson Correlation). A highly significant correlation between the PA-induced shift obtained for immediate and delayed pointing ($r = 0.892$; $p < 0.001$) was found. Taken together, these results show that PA brought about by an immediate pointing task produces almost identical post-adaptation aftereffects for both immediate *and* delayed pointing.

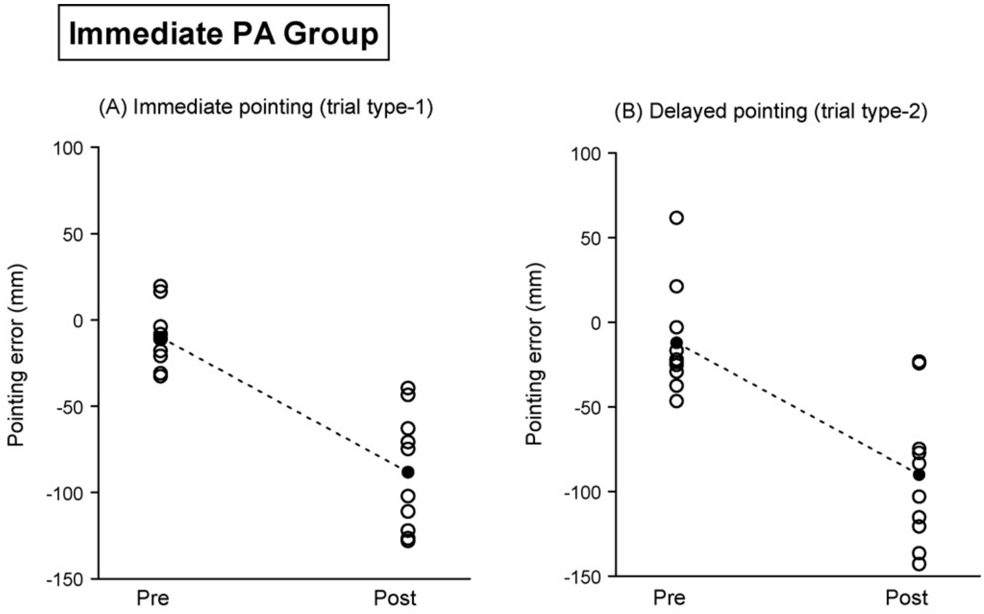

Fig. 1. Experiment 1—Prism adaptation with immediate pointing. Constant error before and after prism adaptation: filled circles represent the mean across all subjects, open circles represent values from individual subjects. (A) Immediate pointing. (B) Delayed pointing.

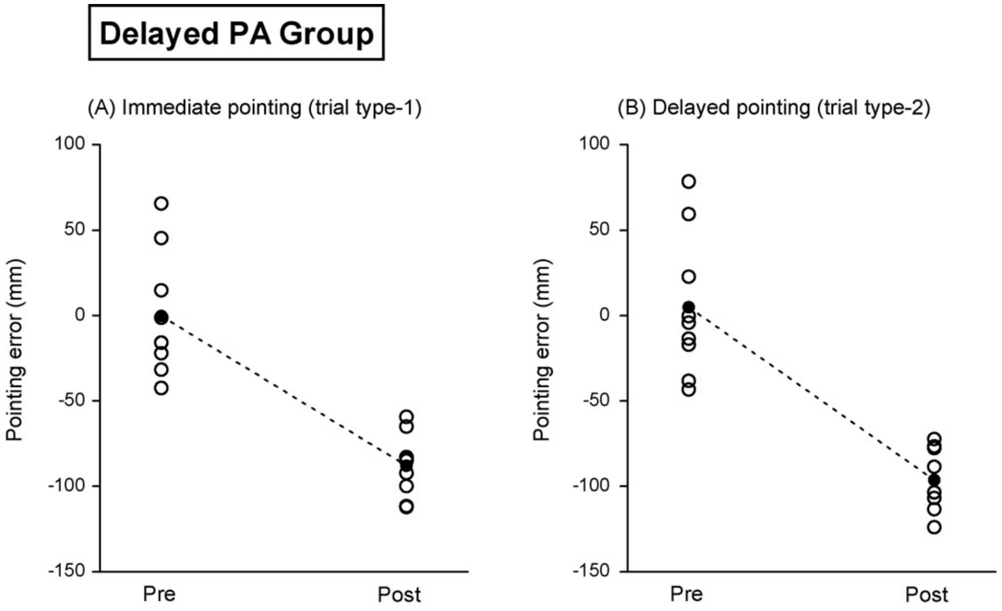

Fig. 2. Experiment 2—Prism adaptation with delayed pointing. Constant error before and after prism adaptation: filled circles represent the mean across all subjects, open circles represent values from individual subjects. (A) Immediate pointing. (B) Delayed pointing.

3.2. Experiment 2—Effects of delayed PA on immediate and delayed pointing accuracy

Once again, we found that PA (this time using a delayed pointing task) led to a significant leftward shift of the pointing response in both conditions [immediate condition: ($t(8) = 8.402$, $p < 0.001$); delayed condition: ($t(8) = 9.506$, $p < 0.001$), see Fig. 2]. Although a substantial shift was found for both pointing tasks (i.e. for immediate pointing mean shift = 87.53 mm; S.D. = 31.25; for delayed pointing: mean shift = 101.07 mm; S.D. = 31.90), the PA-induced shift was slightly but significantly greater in the delayed condition ($t(8) = 3.975$, $p = 0.004$). Again a Pearson correlation between PA-induced shifts for immediate and delayed pointing was computed and confirmed that the shifts found for immediate and delayed pointing were highly correlated ($r = 0.948$; $p < 0.0001$).

3.3. Comparison of pointing tasks in Experiments 1 and 2

We found some interesting differences between Experiments 1 and 2 in terms of the degree of PA transfer: PA transferred fully from immediate pointing in the exposure phase to delayed pointing in the post-exposure phase (Experiment 1), but there was a slightly reduced transfer of PA from delayed pointing to immediate pointing (Experiment 2). In the discussion we suggest that these differences might be due to delayed actions being less well-practised than immediate actions. In order to assess this possibility, we computed the variable horizontal error for the immediate and delayed pointing tasks prior to prism adaption and found that the variable error for pre-exposure pointing was significantly greater for the delayed than for the immediate condition (delayed: 37.16 mm; immediate: 28.32 mm; $t(18) = -4.012$, $p = 0.001$). This finding is in line with our explanation presented in the discussion (see penultimate paragraph in Section 4 for more details).

4. Discussion

Significant negative aftereffects and substantial transfer of adaptation effects between immediate and delayed pointing were observed in both experiments. Assuming that post-exposure aftereffects are largely based on visuo-proprioceptive realignment (cf. Redding, Rossetti, & Wallace, 2005) our finding of a significant aftereffect for delayed pointing suggests that the visual information used to guide delayed action is also coded in an egocentric (i.e. proprioceptively anchored) framework. This finding of an almost complete transfer between delayed and immediate pointing is particularly remarkable in the context of many previous studies on visuomotor adaptation which suggested that even slight changes in the motor task can dramatically reduce the transfer between the tasks. For example Baraduc and Wolpert (2002) showed for pointing movements that even changes in the start position are sufficient to induce a 50% reduction in transfer. Scheidt and Ghez (2007) have shown more recently that a post-adaptation shift of 88% is reduced to a shift of only 18% if the task is changed from a combined reach-and-return movement (“slicing-action”) to a one-directional reaching movement (“reach-action”). These findings of reduced transfer between different motor tasks are taken as evidence that distinct brain processes are involved in the different tasks. Our finding of almost complete transfer between immediate and delayed pointing therefore suggests that immediate and delayed actions share to a considerable extent the same visuomotor transformation mechanism. It is currently unclear, however, where the transformation processes for immediate and delayed actions might converge. Although at present we can only speculate, we would like to discuss a number of different possibilities.

In principle, our findings are consistent with the assumption that the very same pathway is used for both immediate and delayed action. However, we will dismiss this possibility since it is in conflict with the observed neuropsychological dissociations, i.e. a patient with VFA is better with immediate than with delayed action (Goodale et al., 1994; Milner, Dijkerman, et al., 1999), whereas the reverse is true for patients with OA (Milner, Paulignan, et al., 1999).

A more promising possibility is that the allocentric information, which is maintained in the ventral stream during a delay period, is used to *re-activate* the retinotopic representation in early visual areas. This re-activation may then begin the visuomotor transformation cascade that is started by direct retinal input in the case of immediate action. Such a re-activation of representations in early visual areas on the basis of allocentric representations in the ventral stream is supported by a recent fMRI study in which visual illusions were found to affect activity in V1 (Murray, Boyaci, & Kersten, 2006). In particular, for two objects of identical angular size, the object that appeared to be more distant and therefore larger activated a greater area in V1 than the object which appeared to be closer and smaller. If we assume with M&G (2006) that such size illusions arise in the ventral stream, then the most straightforward explanation of this phenomenon is that V1 receives re-activating input from ventral stream areas. This re-activating mechanism could be used to support a conversion from an allocentric to a retinotopic representation and finally to an egocentric representation, which could be used to provide visual guidance for actions under delayed conditions.

Although such a mechanism would also be consistent with Westwood and Goodale's (2003) finding of an increased influence of visual illusions on delayed actions, this account fails to provide a satisfactory explanation for the paradoxical improvement of delayed action in patients with OA (Milner, Paulignan, et al., 1999). However, in this context, it is important to note that a more recent study found only a relatively mild and gradual effect of delays on visuomotor performance in OA and emphasized the fact that performance in OA, even in delayed conditions, is still significantly worse than that observed for healthy subjects (Himmelbach & Karnath, 2005). The re-activation account also fails to provide a satisfactory explanation for evidence from a recent TMS study (Smyrnis, Theleritis, Evdokimidis, Müri, & Karandreas, 2003), which found that stimulation over PPC interferes with delayed action (delay of 3000 ms) only if the stimulation occurs early in the trial (i.e. 300 ms after stimulus presentation) but not later during the trial (i.e. not after 1500 or 2700 ms).

We can use these conflicting findings, in conjunction with our knowledge that the ventral stream appears to be essential for delayed pointing, to derive some conclusions that can be used to constrain our further speculations. Firstly, the fact that performance in OA and with PPC–TMS is impaired even for delayed action suggests that the signal from the ventral stream does not replace the dorsal stream signal but is combined with it. Secondly, since the performance of patients with OA improves with delay, it can be assumed that the weighting given to the dorsal stream signal in this combined dorsal/ventral representation decreases with delay. Thirdly, the fact that PPC–TMS for delayed action is only effective if applied early during the trial suggests that the PPC-signal is produced early but then sent to another area where the signal is sustained and presumably combined with information from the ventral stream. But where in the brain could this convergence of parietal and ventral input happen? Lee and van Donkelaar (2002) have argued on the basis of their TMS study that the most likely region for ventral–dorsal stream interaction is in the prefrontal cortex. More specifically we would like to suggest the dorsolateral prefrontal cortex (DLPC). This area seems to show the complementary pattern to PPC: late but not early TMS over DLPC decreases the accuracy of delayed saccades (Muri, Vermersch, Rivaud, Gaymard, & Pierrot-Deseilligny, 1996). In addition, the DLPC has known connections with both parietal and inferotemporal areas (Roberts et al., 2007).

Is it conceivable that the visuomotor processes for immediate and delayed action converge much later, i.e. at the stage where visual parameters are mapped onto motor parameters? In this case one might argue that the transfer between immediate and delayed action is observed because PA distorts the same matrix for both conditions, namely the matrix that maps visual parameters onto motor parameters. It is commonly assumed that this mapping occurs in parts of the cerebellum (Glickstein & Yeo, 1990). Given the well-established role of the cerebellum in PA, this assumption seems plausible (e.g. Martin, Keating, Goodkin, Bastian, & Thach, 1996a). However, it is important to keep in mind that unless the visual parameters for delayed and immediate action have been translated into a common code prior to the visuomotor mapping stage it is unlikely that the same matrix for visuomotor mapping can be used and therefore little transfer between those two types of actions would be expected. A recent fMRI study also suggests that transfer in visuomotor adaptation involves more than just the cerebellum (Seidler & Noll, 2008). These authors examined the pattern of brain activity which is associated with the degree of savings at transfer and found a whole cluster of brain areas including the right cingulate gyrus, left superior parietal lobule, right inferior parietal lobule, left middle occipital gyrus and regions in the cerebellum, bilaterally.

Before we conclude we should also comment on one rather mysterious aspect of our findings, namely the asymmetry in transfer observed for Experiments 1 and 2. While full transfer to delayed pointing was observed when PA was restricted to immediate pointing, slightly reduced transfer was observed for immediate pointing following PA restricted to delayed pointing. How can we explain this asymmetry? Presently we can offer only a speculative account which is based on the following observation: while immediate pointing is a highly practised task, delayed pointing is not. This difference in practise means that subjects might well expect to make errors in a delayed task but not in an immediate task. In fact this expectation is supported by our findings. Significantly greater variable errors were found for delayed than for immediate pointing already during the pre-exposure phase (see Section 3.3). Accordingly these different expectations might lead to a difference in how subjects respond to the errors. In the case of an immediate action, subjects might assume that they would be good at this task and therefore attribute any error largely to a task-independent bias in the visuomotor system. Consequently, whatever compensatory strategy they adopted, the same would also be applied to other visuomotor tasks (e.g. pointing under delayed conditions) and therefore full transfer to those tasks would be expected. In contrast, in the case of delayed action, subjects might assume that some proportion of the observed error is specific to the task (e.g. due to a lack of practise with that task or due to the fact that they have to memorize the target location). They may therefore assume that for a more practised task (e.g. immediate pointing) the error is less and consequently less compensation may be required. In this case, less than full transfer might be expected from delayed to immediate pointing. Incidentally this account could also explain the asymmetric intermanual transfer which was reported by Sainburg and Wang (2002). They found that prior adaptation of the dominant hand (presumably more skilled hand) produced significant error-reduction for the non-dominant hand during the exposure phase, but the reverse was not true, i.e. the dominant hand did not benefit from prior adaptation of the non-dominant and thus less skilled hand.

To conclude, our findings show that there is substantial transfer of the post-prismatic aftereffect between immediate and delayed pointing. This suggests that immediate and delayed action use to a large extent the same visuomotor transformation processes.

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