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Figure 1b shows that the endpoints of the reaching movements were shifted either upwards or downwards in the direction of the nearby motion. Target flashes presented well before (for example -940 ms) or well after (for example 470 ms) the motion reversal (at 0 ms) produced systematic shifts in the hand's position. Because the target in these cases was presented sufficiently long before or after the motion reversal, the entire reaching movement—both programming and execution—was performed during unidirectional motion (average movement onset and movement duration were 224 and 262 ms, respectively). For this reason it is unclear whether the motion influenced the programming phase or the on-line phase of the reaching movement, or both.

The target flash presented 235 ms before the moving pattern reversed direction addresses this question: because the average reaction time was 220 ms, motion was in one direction during most of the programming phase and in the opposite direction during the movement. This condition produced a markedly reduced shift in the movement endpoint (grey oval in Fig. 1b). The only way in which the shift in the hand's endpoint could be reduced to this extent would be if the contributions of visual motion to programming and on-line control were approximately equal.

Fast reaching movements were subject to on-line control, which is consistent with previous studies in which the target's location is physically altered at the beginning of the reaching movement¹⁰⁻¹⁴. Because a continuously moving background was present in this first experiment, the data allow a close examination of how the representation of target location is updated over time and how this representation is used to adjust an ongoing response.

The left-hand side of Fig. 2a shows the average hand trajectory for one subject when there is downward visual motion near the target during the course of the reach (this sample trajectory is taken, in part, from the data point at 0 ms interstimulus asynchrony (ISA) for subject E.L.V. in Fig. 1b; initially the visual motion nearest the target was upwards, but when the target was presented the motion reversed direction, so that the reach was executed during downward motion only). When the trajectory for upward motion (right-hand

same subject as in Fig. 2). Figure 3b shows the difference between these curves, which reveals the influence of the motion reversal on the hand's trajectory. In this case, visual motion is in one direction during most of the programming phase and in the opposite direction during the execution of the reaching movement. Interestingly, the trajectory of the hand follows the same pattern: the hand deviates in the direction of the initial motion and subsequently shifts in the opposite direction, mimicking the motion reversal.

Because there is a significant visuomotor delay, some time must pass before visual information can influence the trajectory of the hand. This delay can be estimated from the data in Fig. 3b. Immediately after movement onset (236 ms), the hand begins to deviate in the direction of the initial visual motion. The hand eventually starts to shift in the opposite direction (arrow in Fig. 3b), reflecting the influence of the motion reversal on the hand. The delay between the actual motion reversal (dashed vertical line at 235 ms) and the moment that the data curve reaches a plateau (350 ms) gives a minimum visuomotor delay of ~114 ms (see Supplementary Information for an alternative method of calculating the delay). The upper limit on the visuomotor delay is ~201 ms, based on the moment (437 ms) at which the average deviation of the hand's position differs significantly from that estimated from the minimum visuomotor delay ($t_{(73)} = 2.05, P < 0.05$); this is consistent with the fact that the hand's relative position becomes negative at 437 ms. (Estimates of visuomotor delay for additional

subjects are provided in Supplementary Information). The range of this estimated visuomotor delay (~114–201 ms) is similar to that for actual changes in target location^{1,10,12,14,15}, indicating that the influence of visual motion on the updating of fast reaching movements occurs on the same time scale as actual changes in target position; that is, motion-generated position reassignment might be equivalent to a shift in the real position of the target¹⁵. This is surprising, because it indicates that information unrelated to the target (extraneous visual motion) might be processed as fast as information specific to the target, such as actual target location.

The present results show that visual motion information can cause shifts in fast reaching movements to the location of a briefly presented, unrelated stationary object. Previous studies have found that goal-directed reaching can, in some circumstances, be influenced by perceptual illusions, indicating that the awareness of a stimulus might determine the behavior^{15–22}. Figure 3b shows that this did not occur in the present experiment. The trajectory of the hand was modified continuously as the direction of visual motion changed. In this particular case, the hand first moved in the direction of the initial motion (for example upwards, after upward visual motion; the first significant deviation of the hand upwards occurred ~35 ms after movement onset). However, the target flash is never perceived to be shifted upwards in this situation; the flash always appears either shifted downwards or not shifted at all⁷. The hand initially moved upwards, which is in a direction opposite to that of the perception. If reaching movements depended on awareness of the target's location, the hand should never have been shifted upwards; clearly visual motion influences the representation of target position for fast reaching movements without requiring explicit awareness of the target's position.

One possibility is that the visual motion influenced the perceived speed or position of the hand. To confirm that visibility of the hand is not necessary, we repeated the experiment while visibility of the hand was occluded. The results (see Supplementary Information) were similar to those of the first experiment (Fig. 1b), indicating that the influence of motion on reaching is not due to the visual representation of hand speed or location.

The influence of visual motion on fast reaching movements is greatly reduced when there are significant cues to the target object's position. For example, when the duration of the target is increased sufficiently, the endpoints of the movements are accurate (Fig. 4a). This is an interesting situation, because when the visual information about the location of the target is first used to guide the reaching movement, the visuomotor system has no knowledge of the duration of the target; in other words, at the beginning of the programming phase a brief target flash is identical to a long one, as far as the motor system is concerned. Therefore, for long-duration targets we might expect the trajectory of the hand to deviate in the direction of the visual motion early in the movement, but then to correct itself as the duration of the target increases. This is precisely what we observed (Fig. 4b). During the initial phase of the reach, the surrounding motion signals influenced the position of the hand. However, when there was continued retinal information about target location, the representation of position was recalibrated and the hand's trajectory was updated on-line. The implication is that for any abruptly appearing object, even one that remains visible, there is an influence of visual motion on the hand's early trajectory. The influence of motion on fast reaching movements (revealed in the first experiment) is therefore not restricted to flashed targets that disappear long before the onset of the hand's movement.

Fast reaching movements ultimately depend on a comparison of target and hand position in a common coordinate system^{10,23,24}, a comparison that is likely to be computed only on demand²⁵. However, information about target location must initially be represented in retinotopic coordinates. If this early representation of space were influenced by motion, we would naturally expect

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subsequent processing that hinges on this information to manifest a similar distortion. Indeed, motion information is known to influ-

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