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TARGET ARTICLE

Movement Adjustments Have Short Latencies Because There is No Need to Detect Anything

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We can adjust an ongoing movement to a change in the target's position with a latency of about 100 ms, about half of the time that is needed to start a new movement in response to the same change in target position (reaction time). In this opinion paper, we discuss factors that could explain the difference in latency between initiating and adjusting a movement in response to target displacements. We consider the latency to be the sum of the durations of various stages in information processing. Many of these stages are identical for adjusting and initiating a movement; however, for movement initiation, it is essential to detect that something has changed to respond, whereas adjustments to movements can be based on updated position information without detecting that the position has changed. This explanation for the shorter latency for movement adjustments also explains why we can respond to changes that we do not detect.

Some thirty years ago, the claim (Keele & Posner, 1968) that it takes more than 190 ms (a normal simple reaction time) to use visual feedback to adjust goal-directed arm movements was challenged. Studies investigating fast adjustments of ongoing movements found delays that were considerably shorter than normal reaction times (Carlton, 1981; Soechting & Lacquaniti, 1983). Latencies of only 110 ms were reported for adjustments to elbow torque in response to a target jump (Soechting & Lacquaniti, 1983). A direct illustration of the shorter latency for

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adjusting movements than for initiating movements is what happens if the target jumps 25 or 50 ms after it appears. If adjustments would have the same latency as the initial responses, the initial movement direction could not be affected by the target jump. However, experiments show that the initial movement direction is in between the first and second target position (van Sonderen et al., 1988). Short latency adjustments are not only found in simple pointing movements, but also in reach-to-grasp movements in response to changes in target position (Paulignan et al., 1991b) or orientation (Desmurget et al., 1996; Voudouris et al., 2013). Why are latencies of adjustments shorter than normal reaction times? To answer this question, we will evaluate various factors that could influence response times.

Donders (1868; English translation: Donders, 1969) has provided a framework to study stages in information processing that determine the time needed to initiate a movement in response to a stimulus. He argued that the reaction time is the sum of the time needed for four stages in information processing, nowadays referred to as *detection*, *identification*, *selection,* and *execution*. Donders defined *detection* and *execution* as the sensory and motor processes that are needed for a simple reaction time task. Together these stages account for the time needed to start a preplanned movement in response to a known stimulus. He used *identification* to refer to additional sensory processing that is needed when the response depends on the stimulus, and *selection* to refer to additional processing that is needed if the movement cannot be (completely) planned in advance. We realize that this division of the response latency in four serial stages is simplistic, and therefore cannot explain all known differences in reaction times. We nevertheless choose this approach as we think it can help us to understand why movement adjustments to changes in the environment have much shorter latencies than the time needed to initiate a movement.

We will link Donders' four stages to experimental results on fast adjustments to target displacements, working our way back from the last stage: execution. In some studies, authors report movement adjustments with latencies above 200 ms (or changes in EMG after more than 150 ms). As such latencies are not faster than simple reaction times, we will not discuss such results in our evaluation of the role of the different stages in fast responses. At the end, however, we will speculate about why movement adjustments are not always fast.

Movement Execution

Donders used the movement execution stage to explain differences in reaction times between different effectors. In this paper, we limit ourselves to arm movements, so the apparatus for initiating a movement is the same as that for adjusting it. However, the state of the motor apparatus differs. When initiating a movement in a typical reaction time paradigm, the muscles are initially inactive and they are not changing length. In contrast, when adjusting an on-going movement the muscles are activated and their properties are changing quickly over time, for instance due to the force-velocity relationship (Hill, 1938). Can this difference be responsible for the difference in latency?

Some properties of fast adjustments seem to indicate that such an effect might play a role. For instance, adjustments that require a prolongation of ongoing muscle activation have a shorter latency than ones that require a switch to activation of the antagonist (Gielen et al., 1984). In accordance with this finding, a tendency has been observed for movement adjustments to have a shorter latency when the target jumped in the direction of the ongoing movement than when it jumped in the opposite direction (Oostwoud Wijdenes et al., 2013). However, it is not certain that the latter result can be attributed to the state of the muscle, because at the time that the adjustment is visible in the kinematics, the arm is already decelerating, so it is very likely that the antagonist was already active at the time the activation of the muscles changed in response to the target jump.

If the state of the muscles were indeed an important factor for the latency of the adjustment, one would expect clear effects of the timing of the perturbation, as the state of the muscles involved varies considerably during the movement. Oostwoud Wijdenes et al. (2011) tested whether the latency depended on the timing of the perturbation in a fast pointing movement, and found that the timing of the perturbation did not influence the response latency (which was always about 100 ms). The earliest perturbations occurred about 70 ms before movement initiation (100 ms after initial target appearance), so the agonist will have been active at the time of the adjustment. The latest perturbations were about halfway through the movement (300 ms after initial target appearance), so adjustments will have occurred when the antagonist was active. The timing of the perturbation did have a large effect on the vigorousness of the adjustment: later perturbations gave rise to much more vigorous adjustments. More vigorous adjustments reach a set threshold in a shorter time, which might explain why shorter latencies were reported for later perturbations in some studies (Reichenbach et al., 2009; Dimitriou et al., 2013).

Altogether, there is little reason to believe that differences at the execution stage, such as the differences in the state of activity of the muscles, are responsible for the fact that latencies of movement adjustments can be much shorter than simple reaction times.

Movement Selection

This stage describes the time needed to select the appropriate response to an identified stimulus. It is well known that the shortest reaction times are obtained when subjects can prepare the response before the stimulus is presented. The larger the number of different response possibilities, the longer the reaction times that are found (Merkel, 1885). If one varies the probabilities of various responses being required, the frequently occurring responses have a shorter reaction time (Hick, 1952; Hyman, 1953), so it is not the number of alternatives that matters, but the likelihood that a certain response is the correct one. That the dependence of response time on relative frequencies arises at the stage of movement selection, rather than at the stage of target identification, is evident from research on eye movements, where such a dependency is present for antisaccades, but absent in (reflexive) saccades. The two kinds of saccades share the processing for target identification, but differ with respect to movement selection because reflexive saccades—by definition—require no selection (Kveraga et al., 2002).

In contrast with normal reaction times, the latency of fast adjustments to changes in target location is insensitive to the number of alternative target locations after the change (Reynolds & Day, 2012), a finding that the authors interpreted as an indication of a subcortical pathway. Interpreted along the lines of the previous paragraph, this result shows that adjusting on-going movements circumvents the need to select an appropriate response. Thus, one of the reasons that adjustments to ongoing movements are faster than normal reaction times is that no time is needed for movement selection. However, adjustments to an ongoing movement are also faster than simple reaction times, in which case the required action is known even before the stimulus is presented, so being able to skip movement selection cannot explain why the latency of adjusting an ongoing movement can be shorter than a simple reaction time.

The above reasoning applies to the very fastest adjustments to ongoing movements. If a cube that one wants to grasp rotates during the reach-to-grasp movement, the hand follows the cube's rotation with a latency of about 115 ms (Voudouris et al., 2013), without response selection. However, if the cube is rotated in such a way that by following its rotation with one's hand one would end up in an awkward grasping posture, subjects do select new grasping points. The consequences of such movement selection can be seen about 45 ms after the initial response, at a latency of about 160 ms, which is still faster than simple reaction times. Moreover, in reaction time experiments, the latency for initiating a movement is more than 180 ms longer than simple reaction times when one has to select a movement instead of simply initiating a prepared response (Hick, 1952).

Thus, experimental evidence show that selection is generally not part of adjusting ongoing movements: the latency is independent of the number of alternatives. This is logical if one assumes that one is adjusting the selected movement in response to updated sensory information. Moreover, even if selection occurs in the adjustment, it increases the time needed to adjust ongoing movements much less than it does the time needed to initiate them. Most importantly, skipping movement selection cannot explain why adjustments to ongoing movements have a shorter latency than simple reaction times, for which movement selection is by definition also skipped.

Target Identification

Most human movements are not directed to an LED in an otherwise dark environment. In general, we make our movements in a rich environment in which many changes occur. Therefore, if something changes, one must first identify whether this detected change involves the target, before generating a response. If the target changes its position after it has been identified, one can generally respond to that change without requiring any further identification. However, when moving toward a target, if the target and several items in the environment exchange positions at the same time, one must identify which of the items is the displaced target to which one must adjust one's on-going movement. In such cases the response latency has been shown to depend on the difficulty of target identification (Veerman et al., 2008). In that study, the target and two nontargets differed in one attribute (e.g., luminance, color, shape) and they were presented simultaneously. Subjects had to move to the target. The target could switch position with one of the nontargets just after movement onset. Thus, both initiating the movement and adjusting the movement required target identification, and both took longer if the difference between the target and the nontargets was decreased. If the difference was very conspicuous, latencies were very similar to single target response latencies.

Comparing situations in which the target differed from the nontargets by various attributes, Veerman et al. (2008) noticed that subjects could adjust their movements with a 50 ms shorter latency when the target could be identified on the basis of luminance, orientation and size than for targets for which subjects had to determine the color, form or texture. The difference seems to correspond with the distinction between the magno- and parvo-cellular pathways, respectively. This distinction is specific for fast adjustments, as the reaction times did not differ between these two categories. Moreover, the latencies for adjusting and initiating the movements were not correlated (across subjects). These results show that although one might intuitively expect no differences between adjusting ongoing movements and initiating new movements at the stage of target identification, there are such differences. These differences are interesting and not yet completely understood. However, such differences cannot explain why movements can be adjusted with much shorter latencies than they can be initiated, as there is no need for an identification stage in simple reaction time tasks and single target position changes.

Target Detection

When asked to initiate a movement toward a target as soon as it appears, the decision to start a movement is based on detecting the appearance of the target. Target detection involves the comparison of the output of sensors at two moments in time. A well-known example is the bilocal motion detector, for which a minimum detection time (for high velocities) has been estimated to be 45–85 ms (depending on the subject, van de Grind et al., 1986). The detection time becomes longer for lower velocities, resulting in longer reaction times (Smeets & Brenner, 1994). Detection generally leads to a conscious percept, but this percept is not necessary for a reaction to occur. For instance, if directly after the appearance of the target another stimulus is presented, this second stimulus can suppress the conscious percept of the target, without affecting the initial reaction (Schmidt, 2002).

Donders (1868, 1969) could not think of experimental reaction time paradigms that did not require target detection, and therefore could not estimate how much time was involved in this stage. As argued in the previous paragraph, initiating a movement in response to a change in target location without detecting the change is impossible. However, for adjusting an ongoing movement it is not necessary to detect the change in target location, because after selecting a target, the only thing that is needed to reach the target is a continuous update of the current location of this target (Brenner & Smeets, 2011). When the target of an ongoing movement changes its position, it is thus theoretically possible (and experimentally confirmed; Gritsenko et al., 2009) to adjust that movement to the current location of the target without being able to report that the target's location changed. Is the fact that we can omit the detection stage the reason that we can adjust our movements with such a short latency? In this section we will review results obtained with several experimental paradigms that suggest that this is indeed the case.

Transient changes in position are easy to detect. One might expect that this easy detection would help to reduce the latency, just as easy identification led to faster responses (see previous section). However, this is not the case. It has been shown that subjects can adjust their movements to a new target position even if the change in target position remains unnoticed (Goodale et al., 1986; Pélisson et al., 1986;

Prablanc et al., 1986). These authors made the displacement difficult to perceive by applying the change at the moment of peak velocity of a saccade, and checked at the end of a session that subjects indeed could not report the displacement. The original studies that demonstrated movement adjustments to unnoticed changes in target position did not claim to provide precise latencies of these adjustments. One of the difficulties in determining latencies in these experiments is that the saccade that masks the jump presumably also delays determining the new target position until the eye slows down. In later work, again using verbal report as a measure of detection, Prablanc & Martin (1992) argued that the latencies of responses to undetected target jumps might be as short as 105 ms. Gritsenko et al. (2009) explicitly studied whether detection of the jump (as reported verbally after each trial) was related to the latency of the adjustment. They also applied the jumps during saccades, but used target jumps of different amplitudes. In their experiment, large target jumps (>10°) were frequently detected, in contrast to smaller jumps. The latencies of the fast adjustments were independent of the size of the jump. Thus, adjustments can be very fast, irrespective of whether the detection of the jump is suppressed by a saccade.

Another paradigm to prevent detection of the jump is to use a method know from change-blindness research (Simons & Rensink, 2005): present a blank screen during a short interval between the disappearance of the target from the original location and its reappearance at the new location. Oostwoud Wijdenes et al. (2014) found that introducing a blank screen did not lead to longer latencies, as one would expect if detection were important for having short latencies. They reported the opposite finding: introducing a blank screen (and thus making the jump less easy to detect) reduced the latency even further. This resembles effects found in the saccade literature: introducing a gap between fixation offset and target onset can lead to so-called express saccades with latencies comparable to those of fast adjustments (Fischer & Ramsperger, 1984, 1986).

Even for a clearly visible change in target position, the experimental evidence shows that detecting the change is not part of the information processing for adjustments. In an experiment by Castiello et al. (1991), subjects were asked to grasp a target object that could switch position and to give a vocal response as soon as they noticed that the target changed location. The vocal response to the change in location had a slightly longer latency than a vocal response to the initial target appearance. The motor latency for the adjustment was more than 200 ms shorter than the initial reaction time. Thus the adjustments are probably made before the change in position is detected.

The above-mentioned findings suggest that something at Donders' detection stage is responsible for the fact that latencies of movement adjustments can be much shorter than simple reaction times. But how is it possible to respond to a change that one has not detected? Of course some processes in the detection stage cannot be avoided; neither when initiating nor when adjusting movements. For instance, there is no way to circumvent the time taken by retinal processes or the conduction times in the optic nerves. However, there is no need to actually detect a change in stimulus location to respond to the new location.

This response to a changed position without detecting the change might seem a strange claim. We will therefore illustrate how it can work with an example from outside the field of fast motor responses. The sun is moving across the sky at such a low angular velocity (0.25 ‘/s) that the motion detectors of our visual system cannot detect its motion; the human detection threshold is 1.5 ‘/s at best (Johnson & Leibowitz, 1976). Nevertheless, we can deal with its changing position. For instance, we are able to walk in the direction of the sun for hours, following a gently curved trajectory, simply by keeping our body directed at the sun. Keeping one’s body directed at the sun while the sun is moving is a simple task that does not require a decision to respond. It does not require detection of motion; it does not even require a brain, as even sunflowers can do so.

For goal-directed movements, we assume that the estimated target position is constantly being adjusted on the basis of updated visual information (Brenner & Smeets, 2011). Thus, with every action potential that is somehow related to the location of the target (such as signals pertaining to its position on the retina or to the orientation of the eyes) the estimate of the target’s position will shift a little. Such small shifts can start influencing one’s actions well before the change in neuronal activity becomes large enough and lasts long enough to make one consciously or unconsciously ‘realize’ that the pattern of activity has changed. Before discussing this in more depth, we will first consider why some adjustments of ongoing movements do not have considerably shorter latencies than simple reaction times.

Why Aren’t All Adjustments Fast?

Donders’ framework has helped us to identify target detection as being the stage in the information processing that is required for movement initiation in a simple reaction-time task, but can partly be skipped for movement adjustments in response to a change in target position. Having identified this stage, we now understand why some authors find adjustment latencies of more than 200 ms (Boulinguez & Nougier, 1999; Boulinguez et al., 2001; Johnson et al., 2002; Schmidt et al., 2006). It is essential for a fast adjustment that the change does not need to be detected. Common to the papers that do not find fast adjustments is that they used a darkened room and presented a new target position by extinguishing a light at one position and illuminating one at another position. In this situation, one may expect considerable visual persistence, so the extinguished target does not ‘disappear’ immediately. If a trace of the target remains visible at the initial location, the new target needs to be detected before further processing is possible. One study compared adjustments to target jumps in a dark and a structured visual environment (Turrell et al., 1998). In line with our reasoning, they found that adjustments of goal-directed movements (their direction-amplitude condition) occurred earlier when movements were performed in a structured environment than when performed in the dark.

A similar reasoning might explain an intriguing result reported for reach-to-grasp movements. In a dimly lit room Paulignan and coworkers found a much longer latency to respond to a change of size than to a change of position (Paulignan et al., 1991a; Paulignan et al., 1991b). We propose that the reason is that to present a change of size, the authors used two nested translucent objects, a narrow one presented above a wide one. The experimenter indicated using LEDs under the objects which one was the target. In this configuration, it is inevitable that the nontarget object is still visible due to scattered light. Furthermore, subjects had to take the presence of the other object into account to grasp and lift the target successfully. Therefore, it is very likely that detection of a new target is part of the information processing for this task. For the experiment on changing position, the new target was at a different location, so there was no illumination of the previous target and no need to consider it in the action. Subjects could easily interpret the newly lit target as the same target at a different location.

In our view, the essential distinction between adjusting and initiating is not whether the hand is moving or not, but whether the subject has detected and selected a target and is actively directing ones hand to that target or not. One can also direct ones hand to a target while not moving toward it: by pointing. In this case one is actively keeping the hand position aligned to the target position. If the target position changes, detection of this change is not needed to adjust the hand position, one can just keep ones hand pointing at the target. In such a situation (e.g., the experiment of Reynolds & Day, 2012) subjects can adjust their pointing direction with the same short latency as the latency with which goal-directed movements can be adjusted.

Control Strategy

We will end this review by relating the fact that some information (a detectable change in position) is involved in generating a movement, but not in adjusting the same movement, to a possible control strategy involving continuous feedback. To start a movement, one needs information about the target's position, and one needs to detect some signal indicating that one should start to move. To control that movement, a specification of the goal-location may be combined with a gain specifying how vigorous adjustments should be (Liu & Todorov, 2007). Both the specification of the target's location and the gain may vary over time. The goal location is continuously updated on the basis of visual information (Brenner & Smeets, 2011). The gain is to some extent under voluntarily control (Day & Lyon, 2000), and increases during the movement so that later perturbations result in more vigorous adjustments (Oostwoud Wijdenes et al., 2011).

Normally, according to Donders' scheme, movements are initiated after first detecting the target and then determining its location. That localization takes additional time might seem counterintuitive, but is in line with the results of studies on the localization of moving targets at the time of a flash. In such experiments, the target is perceived at a location that it will only reach about 50 ms later, which can be explained by a localization process that only starts after the flash detection (Brenner & Smeets, 2000; Brenner et al., 2006). The idea that localization takes additional time yields an interesting prediction. If subjects use the detection of the target as their go-signal, rather than waiting until they have localized the target, the initial estimate of the target's location will be based on prior information. This is indeed what has been reported: movements with the shortest reaction times tend to start in a default direction instead of to the target (van Sonderen & Denier van der Gon, 1991), just as a startling stimulus elicits a default movement in conditions of response uncertainty (Forgaard et al., 2011).

Once the movement has been initiated, feedback control continuously compares the latest estimates of the locations of target and hand. This control mechanism is responsible for the initial adjustment to any change in hand or target position, without requiring detection of this change. It also explains why movement selection does not play a role in generating adjustments: the response is fully determined by the gain and actual positions. The assumed flexibility of the gain is in line with results showing that the initial adjustment is to some extent under voluntarily control (Day & Lyon, 2000), and later perturbations result in more vigorous adjustments (Liu & Todorov, 2007; Oostwoud Wijdenes et al., 2011). More complicated responses such as moving in the opposite direction than the jump (Day & Lyon, 2000; Johnson et al., 2002) or stopping the movement as soon as the target jumps (Pisella et al., 2000) are possible, but their latency is longer; they only kick in after the initial adjustment in the direction in which the target jumped.

The feedback control requires not only an estimate of the location of the target, but also an estimate of the hand's position. Therefore, one expects similar fast adjustments to perturbations of the (estimated) position of the hand. Indeed, fast adjustments are also found if visual feedback about the hand is perturbed (Brenner & Smeets, 2003). The gain of such adjustments is time-dependent and can be updated on the basis of information obtained during the movement (Dimitriou et al., 2013). If the hand's position is perturbed mechanically, the hand position as estimated from kinaesthetic information changes. In that case too, the (fast) responses are time-dependent, with early adjustments to mechanical perturbations being stereotyped and less tailored to task demands than later ones (Gielen et al., 1988; Smeets et al., 1995; Mutha et al., 2008; Nashed et al., 2012; Pruszynski & Scott, 2012; Nashed et al., 2014). The control strategy described in this section is consistent with a large range of experimental results, the most important being that adjustments to ongoing movements are faster than initiating new movements.

Conclusion

We conclude that the reason that response times for adjusting a movement to a change in target position are shorter than for initiating a movement is that for movement adjustments the target displacement itself does not have to be detected, whereas for movement initiation the detection is needed. The undetected displacement of the target can result in movement adjustments because the estimate of the target's position is continuously updated, independent of any change-detection process. We propose that detecting that the target appeared or was displaced combined with estimating its position takes considerably more time than the time it takes to update its estimated position.

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