

Manual chronostasis: Tactile perception precedes physical contact

Kielan Yarrow^{1,*} & John C Rothwell¹

1. Sobell Department of Motor Neuroscience and movement disorders,
Institute of Neurology,
U.C.L.

Running head: Manual Chronostasis

*Author for correspondence:

Kielan Yarrow,
Sobell Department of Motor Neuroscience &
Movement Disorders,
Institute of Neurology,
8-11 Queen Square,
London WC1N 3BG.

Tel: 020 7837 3611 x 4110/4114

Fax: 020 7278 9836

Email: k.yarrow@ion.ucl.ac.uk

Summary.

When saccading to a silent clock, observers sometimes think that the second hand has paused momentarily. This effect has been termed *chronostasis* and occurs because observers overestimate the time that they have seen the object of an eye movement [1]. They seem to extrapolate its appearance back to just prior to the onset of the saccade rather than the time that it is actually fixated on the retina. Here, we describe a similar effect following an arm movement: subjects overestimate the time that their hand has been in contact with a newly touched object. The illusion's magnitude suggests backwards extrapolation of tactile perception to a moment during the preceding reach. The illusion does not occur if the arm movement triggers a change in a continuously visible visual target: the time of onset of the change is estimated correctly. We hypothesise that chronostasis-like effects occur when movement produces uncertainty about the onset of a sensory event. Under these circumstances, the time at which neurones with receptive fields that shift in the temporal vicinity of a movement change their mappings [2-4] may be used as a time marker for the onset of perceptual properties that are only established later.

Results and discussion.

Many people recognise the “stopped clock” illusion. It has recently been measured experimentally as the subjective lengthening of a post-saccadic stimulus, and termed chronostasis [1]. Observers saccaded to a numeric display. The first number they saw was a “1” that remained visible for 400-1600 ms. This then changed to “2”, “3” etc., with all subsequent digits displayed for one second each (see Figure

1(A)). Subjects judged whether the “1” had been seen for more or less time than the other digits. Compared with a condition in which no eye movement was made, subjects overestimated the time they had seen the saccadic target (“1”). The amount depended upon the size of the preceding eye movement: for small movements of 22°, subjects overestimated by about 120 ms, increasing to 190 ms for larger movements of 55°. We suggested that the onset time of the post-saccadic stimulus had effectively been antedated to a moment just prior to saccade initiation.

A key question is whether chronostasis is specific to saccades. Data favouring this position comes from a failure to detect chronostasis in a recent case study of a patient with congenital ophthalmoplegia (weak eye muscles) who made rapid head movements in compensation for her deficit [5]. In contrast to this, Hodinott-Hill et al employed a modified procedure (intended to reproduce the “dead phone” illusion) and reported a chronostasis-like effect when subjects were required to match the duration of auditory stimuli following a key press and a shift of spatial attention [6]. However, both studies are difficult to compare directly with the initial demonstration of saccadic chronostasis. For example, the variability in data from individual subjects [1] suggests that results from single case studies cannot necessarily be taken as representative of larger groups. Regarding the study of Hodinott-Hill et al, the problem lies in knowing exactly when the shift of attention occurred. The most straightforward interpretation places this event *within* the critical temporal interval that was being judged, offering a challenge to current accounts of dual-task time judgement performance [7-9] but raising an important methodological difference compared with the saccadic chronostasis procedure. One recent report does appear more directly comparable with saccadic chronostasis experiments. Park et al used a counter like that shown in Figure 1(A) and triggered the initial change of number directly from a finger movement (a

mouse key press) [10]. They found a chronostasis-like effect of around 100 ms for this visual stimulus. However, they did not investigate movements of different extents. Here, we address the issue of generality by extending the design of the original saccadic chronostasis procedure to examine arm movements to a tactile stimulus in a large number of subjects. Will reaching to touch a new object cause us to overestimate the period for which we have felt it? If the answer is yes, then does the effect depend, like saccadic chronostasis, on the extent (and therefore duration) of the preceding movement?

Figures 1(B) and 2(A) show the time course of an experimental trial and the layout of experimental apparatus respectively. Subjects reached to a strain gauge mounted upon a vibrator that could vibrate (0.5 mm) at 60 or 120 Hz. Three types of movement were made: long (50 cm), short (15 cm) and double (start from the “long” point, touch down briefly at the “short” point, then continue to the target). Releasing a switch initiated data acquisition for the trial and caused a target vibrator to begin oscillating at 120 Hz. It continued to oscillate at this rate for a variable period such that it was always in this state when subjects first touched it. This was followed by an alternating pattern of vibration at 60, 120, and then 60 Hz, each applied for 1000 ms. For subsequent analysis, first interval presentation times were adjusted to reflect the time the target strain gauge had actually been touched on a given trial by subtracting the time for which the hand had been in motion. Figure 2(B) shows signals recorded on a single trial. In a stationary control condition, subjects simply rested their hand on the target strain gauge and the experimenter initiated the same sequence of fast and slow vibrations. Subjects judged whether the time they had felt the first period of vibration (120 Hz) was longer or shorter than that for which they experienced the later reference intervals.

Figure 3(A) shows mean subjective durations (estimates of the time judged equal to the subsequent reference stimuli) in all four conditions. In the static arm control condition, subjects slightly overestimated the duration of the first period of vibration (942 v. 1000 ms, $t = 2.49$, $df = 23$, $p = 0.02$). However, when subjects reached to touch the target, the effects were much larger: they overestimated the duration of the first period of vibration by 90-120 ms *relative to control* (Fig. 3(A)). This observation was confirmed by ANOVA ($f = 20.41$, corrected $df = 2, 46$, $p < 0.001$) and Bonferroni-corrected follow ups, which showed significant differences individually between each movement condition and control. The small trend for estimates to be lower in long and double move conditions relative to the short move condition was not significant.

These results demonstrate a chronostasis-like effect for reaching movements. The situation appears analogous to saccadic chronostasis, with one difference. In saccadic chronostasis, the size of the effect scales (near linearly) with the size of the saccade. Such duration-dependent scaling would lead us to expect a difference of around 120 ms between the short and long reach conditions in the current experiment, far greater than that actually obtained. Power exceeded 0.99 to detect this difference as a post-hoc comparison ($\alpha = 0.008$). For saccades, chronostasis seems to start over 50 ms before the eyes move and increases with the amplitude of the saccade. With arm movements, chronostasis is independent of movement extent; a similar antedating interpretation would place its onset at some point mid-way through the reaching movement.

Although this perceptual effect appears to depend upon movement of the arm, two other factors may have contributed. Firstly, the pressure exerted upon the vibrating target strain gauge was not equated for reaching and resting (control)

conditions, being greater in the former case. Secondly, visuo-motor factors such as an imprecise visual assessment of the point at which the hand made contact with the target (i.e. some variant of the “representational momentum” effect [11]) or a planned but suppressed eye movement may have influenced our results. In reaching movements where eye position is initially specified but subsequently unconstrained, the eye tends to move before the hand [12]. If eye movement planning were important, we would therefore expect the effect to have shown dependence upon the extent of the preceding reach, which it did not. However, it is conceivable that a saccade was planned and suppressed in response to the sight of the hand crossing the point of fixation, which would have occurred at a similar time relative to vibrator contact in all reach conditions.

In order to exclude the role of these factors we conducted a control experiment where subjects made short (15 cm) reaches to the vibrating target with and without vision of the arm. The latter was controlled using light occluding goggles to obscure vision from the onset of the arm movement (i.e. release of the “home” switch) to the end of the stimulus sequence. We also added a second static arm condition in which subjects pressed on the target strain gauge with the same force typically exerted following their reaching movements in order to assess any potential pressure confound. For this control experiment the vibration sequence was changed to a 120 Hz oscillation, followed by a pause, followed by a second 120 Hz reference oscillation with which comparisons were made. The reference interval (and pause between variable and reference intervals) were shortened to 500 ms, because briefer durations are estimated with less variability [13]. Results are shown in Figure 3(C) and demonstrate a robust difference of approximately 75 ms between both static and both reach conditions ($f = 18.146$, corrected $df = 2, 18$, $p < 0.001$; for individual

comparisons between static/reach conditions, all $p < 0.05$ after Bonferroni correction). Figure 4 shows average signals recorded across movement trials for a typical subject.

A second set of experiments was designed to assess whether reach-dependent chronostasis would extend from tactile to visual stimuli, as suggested by one recent study [10]. In those experiments, subjects initiated a change in a visual target by pressing a switch on which their hands rested. Subjects overestimated the duration of the subsequent visual interval. We therefore modified our reaching task in two ways. Firstly, the screen around the fixation cross now changed colour to provide variable-duration and reference intervals for comparison. Secondly, subjects initiated this sequence by moving their hand and touching a switch. Control blocks of trials were included where no movement was made, with the sequence started by the experimenter. Figure 3(B) shows the results of a first visual experiment in which variable-length and reference intervals were defined by the entire fixation window being displayed in white (entire sequence from key press: white, black, white, black; see Figure 1(C)). In the no movement condition, subjects accurately judged the duration of the first interval (985 ms v. 1000 ms; $t = 0.810$, $p > 0.05$). However, in contrast to the results with the tactile stimulus, reaching with the arm had no effect on subjects' judgement of duration ($F = 1.997$, $p > 0.05$). This failure to obtain chronostasis is unlikely to relate to experimental power, which was 0.97 to detect a difference of 90 ms (smallest effect obtained in experiment 1) as a post-hoc comparison ($\alpha = 0.008$; estimated based on the comparison with the greatest variability). Movements were slightly slower in this experiment (see legend, Figure 3) but this fact is unlikely to have eliminated chronostasis. In our first (tactile) experiment, scatterplots of effect size against average movement time were produced and correlation coefficients calculated across subjects. Neither correlations ($r = -0.056$

for short movements, $r = -0.134$ for long movements) nor visual inspection of scatterplots suggested a relationship between movement speed and effect magnitude. An identical analysis was employed in this visual experiment, again yielding only a slight and non-significant trend for correlations to show the predicted negative relationship (short: $r = -0.067$; long: $r = -0.212$).

We were concerned about the lack of chronostasis effects in this experiment, given previous positive results [10]. We therefore conducted two further experiments to address this discrepancy. In the first, we repeated our previous static control and 15 cm short reach conditions, and added a third condition (based on ref [10]) in which subjects initially rested their finger on the target switch, then depressed it (initiating the stimulus sequence) following a verbal cue from the experimenter. A shorter (500 ms) reference interval was used. The results are shown in Figure 3(D). No effect was obtained in either movement condition relative to control ($f = 2.604$, $p > 0.05$) despite experimental power of 0.99 (both comparisons) to detect a difference as small as 60 ms. We therefore considered whether the intensity and spatial extent of our stimulus (a sizeable fixation window changing from black to white) might have nulled any effect in the key press condition (in [10] a small black counter on a grey background was used). In the second experiment, we assessed the same movements, using a small (0.8°) square stimulus at the centre of the fixation cross. It changed from dark grey to light grey to mark time intervals, with the rest of the fixation window coloured medium grey. Figure 3(E) shows that there was once again no effect ($f = 0.76$, $p > 0.05$; power > 0.8 to detect a 60 ms difference). The reason for our failure to replicate is unclear at this point. Possible factors include posture, the precise nature of the stimulus sequence and its reference duration. Our data suggest that any key press effect may be fragile, however, given that such factors do not substantially affect

reach-dependent tactile chronostasis (c.f. earlier experiments) or saccadic chronostasis [Yarrow, Johnson, Haggard and Rothwell; submitted].

Comparing across experiments, reach-dependent chronostasis was clear with a tactile (vibratory) stimulus, but there was no reliable effect when subjects estimated the duration of a visual stimulus that was fixated throughout the arm movement. We therefore suggest that the physical (as opposed to sensorial) onset of the post-movement stimulus must be uncertain for chronostasis to occur. In the tactile experiments, subjects perceived the state of the target object only when they touched it (its sensorial onset) but had no accurate information about its prior physical state, i.e. the moment at which it actually began to vibrate. The same is true for saccadic chronostasis. The saccadic target is accurately perceived only at the end of the saccade while the true onset of the change could have been at any time during the saccade. In the present visual experiments there was no uncertainty about stimulus onset because subjects continuously fixated the stimulus whilst the arm was moving providing constant information about when it changed colour. Anecdotally, this situation is reminiscent of one context in which the present authors have never experienced the stopped clock illusion; when a ticking second hand can easily be heard. In this case, uninterrupted information from the auditory channel about the precise time of clock movement may be being used in preference to uncertain visual cues.

Can a common mechanism account for chronostasis-like effects arising for different effectors and modalities? Hodinott-Hill et al have suggested that the explanation may be arousal, which is known to influence time estimation [6,14,15]. We question whether arousal can explain previously published data [1,16]. The present data also offer no support for this explanation. It is not clear why a vibrating

tactile stimulus (or preceding movement) should be highly arousing while an obvious colour change (black to white) for a large section of space around the fovea (preceded by the same movement) should not be.

For chronostasis following saccadic eye movements we previously suggested a possible link with predictive remapping processes observed in monkey lateral intraparietal cortex [1]. The receptive fields of cells in this area shift in advance of an upcoming saccade, such that a stimulus at a position the cell will respond to *after the saccade* actually begins to excite it 80 ms before saccade initiation [2]. In fact, predictive receptive field shifts of this type occur in other areas such as the frontal eye fields and superior colliculus [4,17]. They may effectively overcome the sensory delay when a new stimulus arises following a saccade, and permit the advanced planning of future saccades in oculocentric co-ordinates without reliance upon transformations to a spatial frame of reference [4]. It seems plausible that the brain uses these cells' initial (pre-saccadic) responses as a time marker for the true onset of a stimulus at the end of movement. The idea that a specific neural event might subsequently be used as a temporal marker is not new (e.g. "subjective referral" [18]) and remains controversial (e.g. [19]). Nonetheless, we consider it an intuitively appealing account of our saccadic data.

Given the differences between the saccadic and reach-related data, it may be that these effects reflect separate neural mechanisms. However, in the spirit of parsimony, we speculate that manual chronostasis may also rely on predictive mechanisms that maximise post-movement responsiveness. Psychophysical data show that the internal representation of both eye and arm movements is often predictive of actual movement kinematics [20,21] and many bimodal (visual-tactile) cells in ventral premotor cortex show visual receptive fields that move when the arm is repositioned

[3]. Developing these observations into an analogous account of manual chronostasis will, however, require clear data on the timecourse of remapping processes during reaching movements.

Conclusions. Chronostasis is a rather more general phenomenon than the original saccadic data implied and occurs for both saccades and arm movements. It is, however, closely tied to the properties of the stimulus that is being judged. The illusion may reflect specific functional mechanisms relating to the preparation of coordinated action across changes in effector state. As such, further study could provide valuable insights into the sensory-motor control of dynamic behaviour.

Experimental procedures

Short/long/double reaches to a tactile stimulus. Subjective seconds were calculated using logistic regression, with subjects rejected and replaced when a significant fit was not obtained in all conditions. 24 subjects completed six blocks in each condition (fully counterbalanced) a further 6 having been rejected. Subjects fixated an on-screen cross (Sony Trinitron monitor, refresh rate 60 Hz) at the centre of a $\approx 10^\circ$ rectangular window. In the double reach condition, they released a switch (built in house) and reached across to a target strain gauge, briefly touching an intermediate strain gauge en route (F259 button load cell and calibrated load cell amplifier: Novatech Measurement Ltd; D150 amp: Digitimer). In the long reach condition, the intermediate strain gauge was removed. In the short reach condition, it was replaced with the release switch. Fixation was monitored (left eye) using an infra-red eye tracker (Microguide 1000 spectacles, low-pass filtered at 40 Hz). Trials were

automatically rejected if the eye moved outside a 5.3° horizontal region centred on fixation, or if the experimenter noticed a saccade of any size in the on-line display. The tactile stimulus at the reach destination consisted of a second identical strain gauge set upon a vibrator (101 vibrator: Ling Dynamic Systems (LDS); PA25E amp: LDS). The duration of the first 120 Hz oscillation period was controlled using a MOBS procedure [22] (low boundary 600 ms, high boundary 2000 ms, initial presentation random 1100-1500 ms, five reversals to terminate). An accelerometer (Specialised Laboratory Equipment: tremor transducer) was attached to the subject's right (reaching) index finger. Its signal was passed via an AC amplifier (D150 amp: Digitimer; band pass filtered 0.032-300 Hz). All signals were sampled at 200 Hz. The times at which the subject contacted the target strain gauge and contacted/lifted off from the intermediate strain gauge were calculated automatically. By default, a second order 30 Hz low-pass Butterworth filter was applied to both strain gauge signals in both forward and reverse directions to prevent any phase shift (additional options: 10, 20, or 30 Hz high cut frequency; 2nd or 5th order; used occasionally to provide better contact time estimation). Filtered signals were searched for a sudden rise (fall) using a combined criterion: both absolute values and their first derivatives were compared to threshold values based on background signal noise. Estimated contact/release times were displayed and could be adjusted on line. The vibrator and other reach apparatus was set upon a desk isolated from a second desk upon which a chin rest was mounted (eye to screen distance 41 cm). The experiments were controlled by a PC interfaced with a 12 bit A/D card (National Instruments DAQ 1200). To eliminate auditory cues, a second PC generated constant noise (combined 60 Hz and 120 Hz pure tones) delivered via headphones at 80-85 dBa. In a pre-experimental two-forced-choice test, subjects were at chance to detect the vibrator's

movement without touch while fixating and wearing headphones (mean 52% correct; $p > 0.05$).

Reach/blind reach to a tactile target. Based on 10 subjects (blocks presented in random order; pressure control block never first). In the pressure control condition, force levels displayed in all conditions on an oscilloscope (Gould DSO 1604) were used by the experimenter to instruct subjects. Occluding goggles (PLATO visual occlusion spectacles: Translucent technologies) were worn throughout and activated in the blind reach condition. DC Electro-oculography (7A22 amp: Techtronix; low-pass filtered at 100 Hz) replaced infra-red eye tracking. Reference stimulus duration was 500 ms. MOBS parameters were: low boundary 200 ms, high boundary 1000 ms, initial presentation random 400-800 ms, five reversals to terminate. Subjects were again at chance to detect the vibrator without touch in a pretest (mean 52% correct; $p > 0.05$).

Short/long/double reach to trigger a visual stimulus. Based on 24 subjects (3 rejected). Subjects reached to intermediate and target switches rather than strain gauges, and received no masking noise. Reference interval 1000 ms. MOBS parameters were: low boundary 400 ms, high boundary 1600 ms, initial presentation random 800-1200 ms, five reversals to terminate.

Reach to/press to trigger a visual stimulus (x2). Based on 6 subjects (fully counterbalanced). Reference interval 500 ms. MOBS parameters were: low boundary 100 ms, high boundary 900 ms, initial presentation random 300-700 ms, five reversals to terminate. Screen refresh rate was 120 Hz.

References

1. Yarrow, K., Haggard, P., Heal, R., Brown, P., and Rothwell J.C.E. (2001). Illusory perceptions of space and time preserve cross-saccadic perceptual continuity. *Nature* 414, 302-305.
2. Duhamel, J.R., Colby, C.L., and Goldberg, M.E. (1992). The updating of the representation of visual space in parietal cortex by intended eye movements. *Science* 255, 90-92.
3. Graziano, M.S., Yap, G.S., and Gross, C.G. (1994). Coding of visual space by premotor neurons. *Science* 266, 1054-1057.
4. Umeno, M.M., and Goldberg, M.E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive visual responses. *J. Neurophysiol.* 78, 1373-1383.
5. Jackson, S.R., Newport, R., Osborne, F., Wakely, R., Smith, D., and Walsh, V. (in press). Saccade-contingent spatial and temporal errors are absent for saccadic head movements. *Cortex* .
6. Hodinott-Hill, I., Thilo, K.V., Cowey, A., and Walsh, V. (2002). Auditory chronostasis: Hanging on the telephone. *Curr. Biol.* 12, 1779-1781.
7. Lejeune, H. (1998). Switching or gating? The attentional challenge in cognitive models of psychological time. *Behav. Process.* 44, 127-145.
8. Macar, F. (2002). Expectancy, controlled attention and automatic attention in prospective temporal judgments. *Acta Psychol.* 111, 243-262.
9. Zakay, D. (1998). Attention allocation policy influences prospective timing. *Psychon. Bull. Rev.* 5, 114-118.

10. Park, J., Schlag-Rey, M., and Schlag, J. (2003). Voluntary actions expands perceived duration of its sensory consequence. *Exp. Brain Res.* *149*, 527-529.
11. Freyd, J.J., and Finke, R.A. (1984). Representational Momentum. *J. Exp. Psychol. Learn. Mem. Cog.* *10*, 126-132.
12. Prablanc, C., and Martin, O. (1992). Automatic control during hand reaching at undetected two-dimensional target displacements. *J. Neurophysiol.* *67*, 455-469.
13. Allan, L.G. (1979). The perception of time. *Percept. Psychophys.* *26*, 340-354.
14. Treisman, M., Faulkner, A., Naish, P.L., and Brogan, D. (1990). The internal clock: Evidence for a temporal oscillator underlying time perception with some estimates of its characteristic frequency. *Perception* *19*, 705-743.
15. Wearden, J.H., Edwards, H., Fakhri, M., and Percival, A. (1998). Why "sounds are judged longer than lights": Application of a model of the internal clock in humans. *Q. J. Exp. Psychol. B* *51*, 97-120.
16. Rose, D., and Summers, J. (1995). Duration illusions in a train of visual stimuli. *Perception* *24*, 1177-1187.
17. Walker, M.F., Fitzgibbon, E.J., and Goldberg, M.E. (1995). Neurons in the monkey superior colliculus predict the visual result of impending saccadic eye movements. *J. Neurophysiol.* *73*, 1988-2003.
18. Libet, B., Wright, E., Feinstein, B., and Pearl, D.K. (1979). Subjective referral of the timing for a conscious sensory experience: a functional role for the somatosensory specific projection system in man. *Brain* *102*, 193-224.

19. Pockett, S. (2002). On subjective back-referral and how long it takes to become conscious of a stimulus: a reinterpretation of Libet's data. *Conscious. Cogn.* *11*, 144-161.
20. Schlag, J., and Schlag-Rey, M. (2002). Through the eye, slowly: delays and localization errors in the visual system. *Nat. Rev. Neurosci.* *3*, 191-215.
21. Dassonville, P. (1995). Haptic localization and the internal representation of the hand in space. *Exp. Brain Res.* *106*, 434-448.
22. Tyrrell, R.A., and Owens, D.A. (1988). A rapid technique to assess the resting states of the eyes and other threshold phenomena: The Modified Binary Search (MOBS). *Behav. Res. Methods Instrum. Comput.* *20*, 137-141.

Figure legends

Figure 1. Schematic comparing the time course of movement production and stimulus presentation across experiments (single movement conditions).

(A) Typical sequence for previously reported saccadic chronostasis experiments [1].

(B) Sequence for first experiment involving reaching to a vibrating tactile stimulus.

Oscillations are shown at 1/10th actual rate.

(C) Sequence for first experiment involving reaching to trigger a change of screen colour.

Figure 2. Apparatus and signals recorded in first experiment involving reaching to a vibrating tactile stimulus.

- (A) Schematic of experimental apparatus showing a trial from a double reach block. The hand is shown resting on (obscuring) the release switch.
- (B) Signals recorded following movement initiation in a typical double reach trial and displayed to the experimenter for modification/rejection. Top = accelerometer; top middle = target strain gauge; bottom middle = intermediate strain gauge; bottom = eye position. Vertical lines show computed strain gauge contact and release times (dotted for intermediate, solid for target; see methods). Note that the accelerometer picked up the target strain gauge's vibration following finger contact. No formal calibration was carried out in this experiment, but the experimenter's online display also showed modifiable high/low range values around the eye tracker trace.

Figure 3. Mean subjective duration values in all experiments. Error bars show standard deviations.

- (A) Short/long/double reaches to a vibrating tactile stimulus. Short and long reaches took an average of 251 ms and 370 ms respectively. For double reaches, the first (35 cm) component took an average of 295 ms, the second (15 cm) component an average of 247 ms, and subjects depressed the intermediate strain gauge for an average of 73 ms (total time = 615 ms).
- (B) Short/long/double reaches to a switch that triggered a change of screen colour. Short and long reaches took an average of 311 ms and 448 ms respectively. Double reaches took $349 + 301 + 85 = 735$ ms.
- (C) Visual/blind reaching to a vibrating tactile stimulus. Reaches (15 cm) took an average of 269 ms with vision, 259 ms without. The touch control condition

involved lightly touching the vibrator; the pressure control condition involved the application of force to mimic conditions following a reach.

(D) Reaching to/pressing a switch triggering a white/black colour sequence. Reaches took an average of 294 ms.

(E) Reaching to/pressing a switch triggering a light grey/dark grey colour sequence. Reaches took an average of 299 ms.

Figure 4. Average signals time locked to computed target contact time for reaches made by a single subject in an experiment manipulating the availability of vision. Based on 51 and 66 trials with (A) / without (B) vision respectively. Note that the algorithm was slightly conservative in determining contact time, leading to an underestimation of effect size (true for all subjects). For comparison with eye position signals, the target strain gauge was $> 10^\circ$ from the fixation point. No subject's average trace deviated by more than 1° .

Figure 1 (Yarrow and Rothwell)

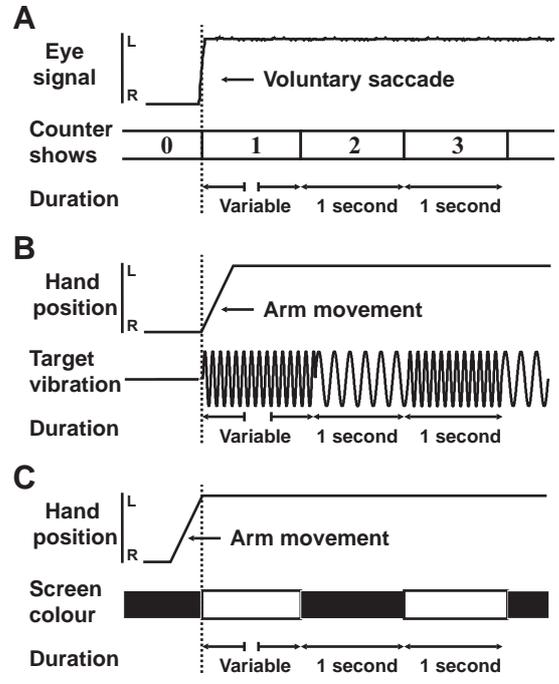


Figure 2 (Yarrow and Rothwell)

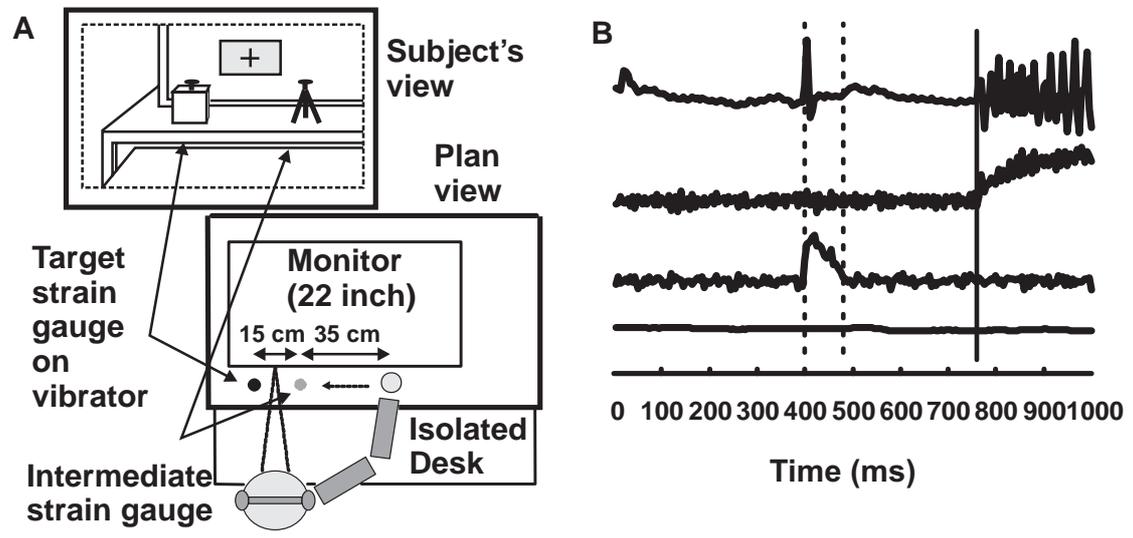


Figure 3 (Yarrow and Rothwell)

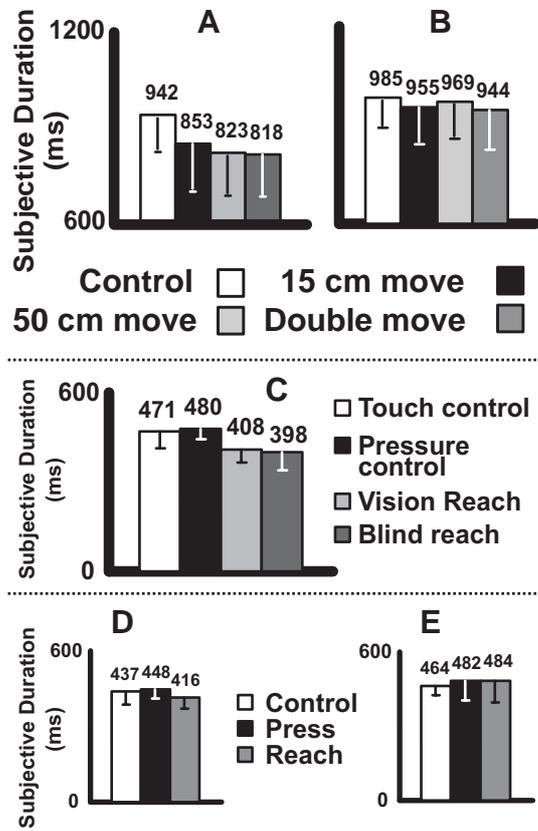


Figure 4 (Yarrow and Rothwell)

