

Changes in posture alter the attentional demands of voluntary movement

Richard G. Carson^{1*}, Romeo Chua², Winston D. Byblow³, Pauline Poon²
and Christopher J. Smethurst¹

¹*Perception and Motor Systems Laboratory, Department of Human Movement Studies, The University of Queensland, Brisbane, Queensland 4072, Australia*

²*Faculty of Physical Education and Recreation, University of Alberta, Edmonton, Alberta, Canada T6G 2H9*

³*Department of Sport and Exercise Science, University of Auckland, Private Bag 92019, Auckland, New Zealand*

Two simple experiments reveal that the ease with which an action is performed by the neuromuscular–skeletal system determines the attentional resources devoted to the movement. Participants were required to perform a primary task, consisting of rhythmic flexion and extension movements of the index finger, while being paced by an auditory metronome, in one of two modes of coordination: flex on the beat or extend on the beat. Using a classical dual-task methodology, we demonstrated that the time taken to react to an unpredictable visual probe stimulus (the secondary task) by means of a pedal response was greater when the extension phase of the finger movement sequence was made on the beat of the metronome than when the flexion phase was coordinated with the beat. In a second experiment, the posture of the wrist was manipulated in order to alter the operating lengths of muscles that flex and extend the index finger. The attentional demands of maintaining the extend-on-the-beat pattern of coordination were altered in a systematic fashion by changes in wrist posture, even though the effector used to respond to the visual probe stimulus was unaffected.

Keywords: movement; posture; coordination; attentional demands

1. INTRODUCTION

Recent debate in the area of human motor control has focused upon the issue of whether general principles and laws of movement coordination may be derived without specific reference to anatomical, mechanical and physiological mechanisms (Kelso 1995). It has been proposed that the stability of coordination is governed by fundamentally abstract, context-specific, informational quantities rather than by particular neuromuscular–skeletal constraints (Kelso 1994). This conjecture is based to some degree on the outcome of a study conducted by Kelso *et al.* (1990) in which subjects were required to synchronize peak flexion of the index finger either on the beat or off the beat of an auditory metronome. The latter condition required that subjects produce a flexion movement midway between each metronome pulse. Kelso *et al.* (1990) noted that all subjects were capable of maintaining the flex-on-the-beat pattern at very high frequencies. In contrast, in the flex-off-the-beat condition the coordination pattern became unstable, and broke down at relatively low frequencies. It transpired that only one of the seven subjects tested was capable of maintaining the flex-off-the-beat pattern through the entire range of pacing frequencies. This subject had adopted a strategy of performing an extension movement in synchrony with the metronome rather than a flexion movement between the beats. The implication of

this finding is that the salient relationship is that which exists between any appropriately designated movement landmark (e.g. finger extension) and an external event. As this critical relationship is held to be strategically rather than anatomically referenced, it has been contended that a pattern of extension on the beat will be functionally equivalent to a pattern of flexion on the beat (Kelso 1994). Some support for this position has been provided recently by experiments showing that spatially distributed patterns of cortical activity are similar during movements that require the synchronization of finger flexion with a periodic signal and during sequences that require the synchronization of finger extension with the signal. It has been argued on this basis that the higher-order planning elements of the two tasks are equivalent (Kelso *et al.* 1998).

There is, however, compelling evidence that the stability of coordination is influenced profoundly by specific neuromuscular–skeletal constraints which determine the ease with which particular movement patterns are performed. Some of these constraints are easily discerned, such as the restriction that certain joints function only as simple hinges. Other constraints are less tangible and arise from complex interactions between the neural and biomechanical properties of the movement system. For example, tasks that require the synchronization of a flexion movement with the beat of a metronome are performed in a more consistent fashion than those that require an extension movement to be made on the beat.

*Author for correspondence (richard@hms.uq.edu.au).

Furthermore, if the frequency of movement is steadily increased, transitions from the extend-on-the-beat pattern to the flex-on-the-beat pattern or to patterns lacking clear structure (phase wandering) are typically observed (Carson 1996; Carson & Riek 1998). It has also been shown that changes in the posture of the limb, that result in alterations in the lengths and orientations of the flexor and extensor muscles, have both predictable and reliable effects on the stability of coordination. Specifically, the frequency at which the extend-on-the-beat pattern is compromised is determined in part by the length of the extensor muscles (Carson 1996; Carson & Riek 1998). Clearly the efficacy with which an action is performed by the neuromuscular–skeletal system determines the stability of coordination. It seems improbable therefore that the higher-order planning elements of movement are not also constrained in a parallel fashion. In the present study, we used a classical dual-task methodology to explore whether the attentional demands of voluntary movement are governed by neuromuscular–skeletal constraints. For the present purposes, we conceive of attentional demand in terms of the categorization introduced by Posner & Boies (1971). This framework includes three interrelated attentional contexts: attention as alertness, including a readiness (or ‘preparedness’) to respond, attention as a limited capacity or resource and attention as selectivity, including the execution of a response in the face of competition from other task requirements.

2. METHODS

The task for which an assessment of attentional demand was sought (the primary task) was one in which participants synchronized either flexion or extension of the index finger on the beat of an auditory metronome. The secondary task, which provided the principal measures from which implications regarding the attentional demands of the primary task were derived, was the detection of a visual probe to which participants responded by depressing a foot switch. The advantage of this approach is that the interpretation of the secondary task performance as an index of attentional demand does not require that one subscribe to any specific model of attentional processing and encapsulates only the assumption of a finite information-processing capacity that does not change across variants of the primary task. As we did not seek to address modality-specific attentional demands, a pedal response to a visual probe stimulus was employed to reduce the potential for within-modality competition (Duncan *et al.* 1997).

(a) *Experiment 1*

Participants were seated at a table, with their right forearm supported in a neutral position by a thermoplastic mould, with the index finger splinted to a lever that rotated about a vertical shaft. A splint secured to the ventral surface of the right index finger prevented motion of the interphalangeal joints. Motion of the index finger about the metacarpophalangeal joint was transduced at 1000 Hz at an analogue to digital interface (DataQ, Akron, Ohio, USA) via a potentiometer mounted coaxially with the shaft. An auditory metronome (50 ms at 2900 Hz) provided pacing for movements of the finger. The illumination (100 ms duration) of a single light-emitting diode (LED) positioned directly in the participants’ line of sight constituted the visual

probe stimulus. Pedal responses to the probe were obtained from the status of a simple foot-switch that was sampled at 1000 Hz.

In an initial session, a critical pacing frequency (CF) was determined for each of nine healthy volunteers. Each individual performed a series of trials (30 s) during which they performed the extend-on-the-beat pattern. If the pattern was maintained throughout the trial, the pacing frequency was increased by 0.25 Hz in the subsequent trial. If the participant showed signs of loss of stability (transitions or phase wandering), the pacing frequency remained the same in the following trial. The CF was defined as the pacing frequency at which the participant failed to maintain the required pattern in three successive trials. The mean CF for all subjects was 2.76 Hz (s.e. = 0.92 Hz).

During each experimental trial of 65 s duration, the frequency of the metronome was held constant at one of two frequencies, = CF–0.1 Hz or = CF+0.4 Hz. Individuals are capable of sustaining patterns of coordination at movement rates above their normal transition frequency, although there is a cost in terms of the performance of other dimensions of the task (Lee *et al.* 1996). Eight probe stimuli were delivered at random intervals during each trial. On average, probes were separated by 8 s. The participants were instructed to react as quickly as possible to the probe by depressing the foot switch and to attempt to maintain the prescribed coordination pattern (extend-on-the-beat or flex-on-the-beat) at the metronome frequency throughout the trial. A total of 40 trials were distributed evenly over two sessions. Within each 20-trial block, the order of presentation of each combination of pacing frequency and coordination pattern was randomized, subject to the constraint that a maximum of two trials in succession could have the same condition.

In order to interpret differences in the performance of the secondary task as variations in attentional load, it is necessary to first ensure that the primary task is performed in an adequate fashion. We employed a number of steps to exclude probe responses elicited when participants had not adhered to the requirements of the primary task in the 4 s immediately preceding a stimulus. In the first instance we applied the Rayleigh test (Mardia 1972) to exclude responses made when the coordination pattern was not stable. We also removed responses made when the relative phase between the stimuli and displacement of the finger did not lie within three confidence intervals (95%) of the target pattern. We also discarded reaction time outliers that were beyond the inner fences of the distribution of response times obtained for each participant. These steps resulted in the retention of 1398 (52.6%) probe responses for further analysis.

(b) *Experiment 2*

The right hands and forearms of a separate group of 12 participants were supported in a neutral position by separate thermoplastic moulds. The base of the mould used to support the hand was pivoted at a point coaxial with the axis of rotation of the wrist. This arrangement permitted the wrist joint to be fixed in one of three positions: (i) 30° flexion, (ii) neutral and (iii) 30° extension, while maintaining the posture of the hand constant, including the thumb. The middle, ring and little fingers were unrestrained. The mean CF (obtained in the neutral wrist position) was 2.79 Hz (s.e. = 0.81 Hz). A single block of 12 experimental trials was performed for each wrist position. The frequency of the metronome was held constant at the CF in each trial. The order of block presentation was counterbalanced across participants. In all other respects, the procedures were identical to those used in experiment 1. Following application of

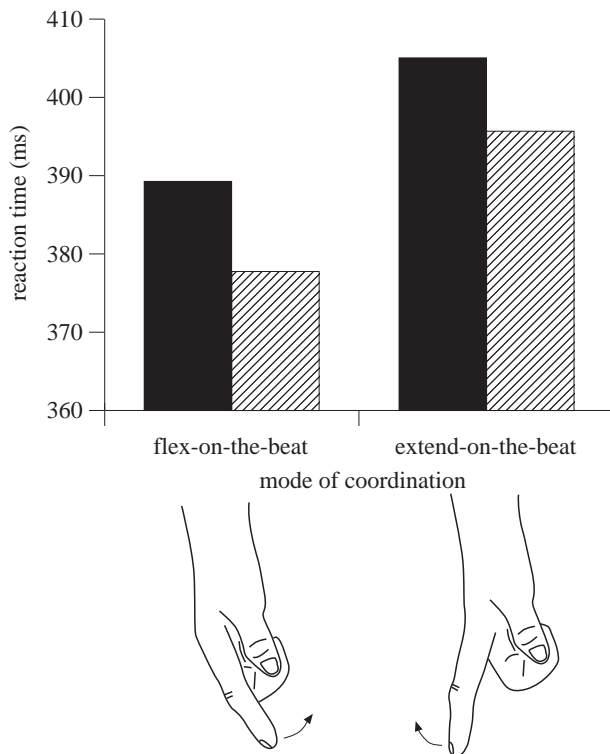


Figure 1. Median probe reaction times obtained in experiment 1 during the flex-on-the-beat and the extend-on-the-beat modes of coordination. The solid bars represent the responses obtained when the movements were paced at the CF - 0.1 Hz. The diagonal hatched bars represent the responses obtained when the movements were paced at the CF + 0.4 Hz. Each mode of coordination is depicted in schematic form in the lower portion of the figure.

the exclusion criteria, 1450 (46.2%) responses were retained for further analysis.

3. RESULTS

The probe reaction times elicited during performance of the flex-on-the-beat pattern were of shorter duration (mean = 383.4 ms, s.e. = 9.13 ms) than those obtained during the extend-on-the-beat pattern (mean = 399.9 ms, s.e. = 9.20 ms) (figure 1). Analysis of variance indicated that this pattern of results was exhibited both when movements were paced at the CF - 0.1 Hz ($F_{1,8} = 8.95$, $p < 0.02$) and when paced at the CF + 0.4 Hz ($F_{1,8} = 11.24$, $p < 0.01$). The magnitude of this effect (Cohen 1969) was somewhat greater when movements were paced at a frequency above the CF ($f = 0.79$) than when paced below the CF ($f = 0.70$).

In a second experiment, we focused on changes in attentional load when the posture of the wrist in the flexion-extension plane was manipulated to alter the operating lengths of the flexor and extensor muscles of the finger that spans the wrist (extensor digitorum communis, extensor indicis, flexor digitorum superficialis and flexor digitorum profundus). On the basis of our previous findings of a selective disruption to the extension phase of the movement following manipulations of wrist and forearm posture (Carson 1996; Carson & Riek 1998), we predicted that the attentional demands of generating the extend-on-the-beat pattern when the wrist was in an

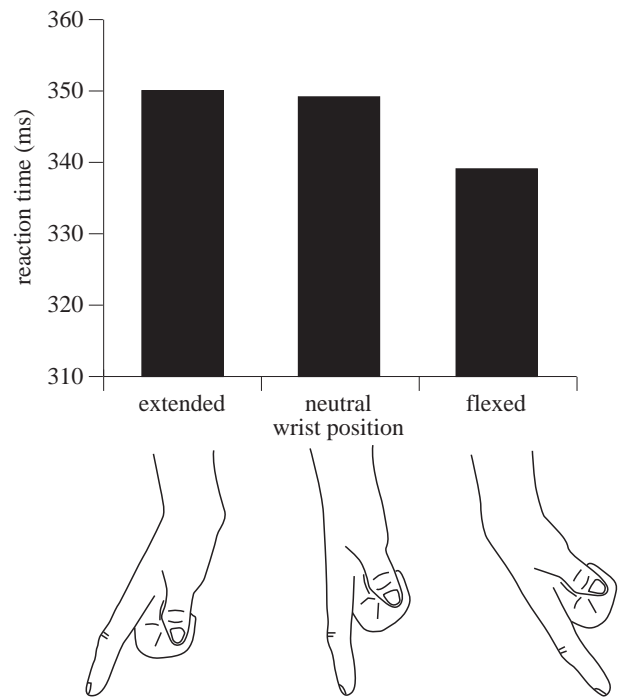


Figure 2. Median probe reaction times obtained in experiment 2 during movements performed when the wrist was fixed in an extended, neutral or flexed posture. All responses were obtained during the extend-on-the-beat mode of coordination. Movements were paced at the CF. Each wrist posture is depicted in schematic form in the lower portion of the figure.

extended (30°) position would be greater than when the wrist was in a flexed (30°) or a neutral position.

The time required to respond to the probe stimulus was greater when the wrist was extended (mean = 350.1 ms, s.e. = 7.36 ms) than when the wrist was flexed (mean = 339.0 ms, s.e. = 7.53 ms) ($F_{1,22} = 3.48$, $p < 0.05$, $f = 0.38$) (figure 2). In contrast, the mean response times obtained when the wrist was in a neutral position (mean = 349.1 ms, s.e. = 7.44 ms) were essentially equivalent to those obtained when the wrist was extended ($F_{1,22} < 1$, $p > 0.20$, $f = 0.04$).

4. DISCUSSION

Our findings demonstrate that the higher-order planning elements of a simple voluntary movement, requiring flexion and extension of the index finger, are determined by the phase of the movement (flexion or extension) that is coordinated with an external signal. They are also impacted upon by changes in posture that alter the length of the muscles that flex and extend the finger. As a result of their phylogenetic origin as anti-gravity muscles, the flexors of the upper limb are stronger than the extensors, requiring a smaller proportion of motor units to be activated in order to produce a given level of force (Vallbo & Wessberg 1993). Unit changes in the firing rate of corticomotoneuronal cells facilitating flexor muscles also result in a greater modification of torque than an equivalent change in cells facilitating extensor muscles (Cheney *et al.* 1991). In addition, flexion (but not extension) of the index finger is assisted by muscles intrinsic to the hand, which receive a high proportion of monosynaptic corticospinal

projections (Phillips & Porter 1977). In contrast, extension of the finger is brought about only by muscles originating in the forearm, the projections to which are known to be less dense and less differentiated than those to the intrinsic hand muscles (Lemon 1988). It appears, therefore, that the greater efficacy with which flexion is generated by the neuromuscular–skeletal system requires that a lower level of attention be devoted to a coordination task that emphasizes the flexion phase of the movement cycle.

The extensor digitorum communis and extensor indicis are the only muscles that generate extensor torques at the metacarpophalangeal joint. Extension of the index finger is thus brought about by the contraction of muscles that have their origin in the forearm. The operating lengths of these muscles and, thus, their capacity to generate force (Gordon *et al.* 1966) vary as a function of the posture of the wrist. The results of our second experiment revealed that, when the extend-on-the-beat pattern was performed with the wrist in an extended posture, probe reaction times were of greater duration than those obtained with the wrist in a flexed posture. It has been demonstrated previously that when the wrist is moved to an extended posture, the extension phase of the movement sequence is disrupted, leading to a decrease in the stability of the extend-on-the-beat pattern. In contrast, the flexion phase of the movement is not modified in this fashion (Carson & Riek 1998). Presumably this is due to the additional contribution to flexion assumed by the intrinsic muscles of the hand, the lengths of which do not change with alterations in the posture of the wrist. It has been estimated that, during metacarpophalangeal joint flexion with simultaneous interphalangeal joint extension, 73% of the resultant moment is accounted for by the action of the intrinsic muscles (Ketchum *et al.* 1978).

The current findings emphasize that simple changes in posture determine the ‘higher-order planning elements’ of coordination. It is evident, however, that the magnitude of the change in attentional demand attributable to alterations in posture is smaller than the difference between the flex-on-the-beat and the extend-on-the-beat patterns of coordination. Recent findings point to significant individual variation in the musculoskeletal geometry of the forearm (Nathan 1992). It is likely, therefore, that variations in attentional demand, arising from changes in muscle length and muscle moment arms brought about by alterations in posture, will also vary appreciably between individuals. In contrast, the neuroanatomical factors that distinguish the flexion and extension phases of upper limb movement are expressed more uniformly.

It is clear that multiple pathways, extending from the visual cortex to the motor neuron, mediate the execution of simple (i.e. pedal) responses to discrete visual stimuli. In the present study, however, the stimulus-driven action of the secondary task was maintained constant throughout. It is likely, therefore, that the neural mechanisms implicated in the observed alterations in attentional demand are directly related to the performance of the primary task. Repetitive finger tapping in time with an auditory stimulus is mediated by activity in the sensorimotor cortex, supplementary motor area, primary auditory cortex and cerebellum (Blinkenberg *et al.* 1996). The extent of the primary motor cortex that is activated increases with the rate of movement (Schlaug *et al.* 1996).

In addition, with rising levels of finger flexion force, there is an initial steep increase in motor cortex activity, reflecting the recruitment of a larger number of small motor units, followed by a further less rapid increase in activity as a smaller number of large units are engaged (Dettmers *et al.* 1995). As a consequence of the lower gain of the extensors, the cerebral activity associated with movements that primarily engage the extensors will be greater than that during movements driven by the flexors. Alterations of limb posture will result in similar changes in the activation of the motor cortex, if an increased level of central drive to the motor neuron pool is required. It is well-known that the cortical representations of muscles overlap broadly (Schieber & Hibbard 1993). We suggest, therefore, that attentional demand in some measure reflects the degree of response competition between the overlapping cortical representations of the muscles engaged in the primary and secondary tasks. The efficacy with which an action is performed by the neuromuscular–skeletal system may thus determine the spatial distribution of activity within the motor cortex and, as a consequence, the degree of interference with concurrent motor responses.

This research was supported by the Australian Research Council and the Natural Sciences and Engineering Research Council of Canada.

REFERENCES

- Blinkenberg, M., Bonde, C., Holm, S., Svarer, C., Andersen, J., Paulson, O. B. & Law, I. 1996 Rate dependence of regional cerebral activation during performance of a repetitive motor task: a PET study. *J. Cerebr. Blood Flow Metab.* **16**, 794–803.
- Carson, R. G. 1996 Neuromuscular–skeletal constraints upon the dynamics of perception-action coupling. *Exp. Brain Res.* **110**, 99–110.
- Carson, R. G. & Riek, S. 1998 The influence of joint position on the dynamics of perception-action coupling. *Exp. Brain Res.* **121**, 103–114.
- Cheney, P. D., Fetz, E. E. & Mewes, K. 1991 Neural mechanisms underlying corticospinal and rubrospinal control of limb movements. *Prog. Brain Res.* **87**, 213–252.
- Cohen, J. 1969 *Statistical power analysis for the behavioral sciences*. New York: Academic Press.
- Dettmers, C., Fink, G. R., Lemon, R. N., Klaus, M. S., Passingham, R. E., Silbersweig, D., Holmes, A., Ridding, M. C., Brooks, D. J. & Frackowiak, R. S. J. 1995 Relation between cerebral activity and force in the motor areas of the human brain. *J. Neurophysiol.* **74**, 802–815.
- Duncan, J., Marten, S. & Ward, R. 1997 Restricted attentional capacity within but not between modalities. *Nature* **387**, 808–810.
- Gordon, A. M., Huxley, A. F. & Julian, F. J. 1966 The variation in isometric tension with sarcomere length in vertebrate muscles. *J. Physiol.* **184**, 170–192.
- Kelso, J. A. S. 1994 The informational character of self-organized coordination dynamics. *Human Move. Sci.* **13**, 393–413.
- Kelso, J. A. S. 1995 *Dynamic patterns: the self-organization of brain and behavior*. Cambridge, MA: MIT Press.
- Kelso, J. A. S., Delcolle, J. D. & Schöner, G. S. 1990 Action-perception as a pattern formation process. In *Attention and performance*, vol. 13 (ed. M. Jeannerod), pp. 139–169. Hillsdale, NJ: Erlbaum.

- Kelso, J. A. S., Fuchs, A., Lancaster, R., Holroyd, T., Cheyne, D. & Weinberg, H. 1998 Dynamic cortical activity in the human brain reveals motor equivalence. *Nature* **392**, 814–818.
- Ketchum, L. D., Thompson, D., Pocock, G. & Wallingford, D. 1978 A clinical study of forces generated by the intrinsic muscles of the index finger and the extrinsic flexor and extensor muscles of the hand. *J. Hand Surg.* **3**, 571–578.
- Lee, T. D., Blandin, Y. & Proteau, L. 1996 Effects of task instructions and oscillation frequency on bimanual coordination. *Psychol. Res.* **59**, 100–106.
- Lemon, R. 1988 The output map of the primate motor cortex. *Trends Neurosci.* **11**, 501–506.
- Mardia, K. V. 1972 *Statistics of directional data*. London: Academic Press.
- Nathan, R. H. 1992 The isometric action of the forearm muscles. *J. Biomech. Engineer* **114**, 162–169.
- Phillips, C. G. & Porter, R. 1977 *Corticospinal neurones: their role in movement*. London: Academic Press.
- Posner, M. I. & Boies, S. J. 1971 Components of attention. *Psychol. Rev.* **78**, 391–408.
- Schieber, M. H. & Hibbard, L. S. 1993 How somatotopic is the motor cortex? *Science* **261**, 489–492.
- Schlaug, G., Sanes, J. N., Thangaraj, V., Darby, D. G., Jäncke, L., Edelman, R. R. & Warach, S. 1996 Cerebral activation covaries with movement rate. *Neuroreport* **7**, 879–883.
- Vallbo, Å. B. & Wessberg, J. 1993 Organization of motor output in slow finger movements in man. *J. Physiol.* **469**, 673–691.

