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# Functionally dissociating temporal and motor components of response preparation in left intraparietal sulcus

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ABSTRACT

To optimise speed and accuracy of motor behaviour, we can prepare not only the type of movement to be made but also the time at which it will be executed. Previous cued reaction-time paradigms have shown that anticipating the moment in time at which this response will be made ("temporal orienting") or selectively preparing the motor effector with which an imminent response will be made (motor intention or "motor orienting") recruits similar regions of left intraparietal sulcus (IPS), raising the possibility that these two preparatory processes are inextricably co-activated. We used a factorial design to independently cue motor and temporal components of response preparation within the same experimental paradigm. By differentially cueing either ocular or manual response systems, rather than spatially lateralised responses within just one of these systems, potential spatial confounds were removed. We demonstrated that temporal and motor orienting were behaviourally dissociable, each capable of improving performance alone. Crucially, fMRI data revealed that temporal orienting activated the left IPS even if the motor effector that would be used to execute the response was unpredictable. Moreover, temporal orienting activated left IPS whether the target required a saccadic or manual response, and whether this response was left- or right-sided, thus confirming the ubiquity of left IPS activation for temporal orienting. Finally, a small region of left IPS was also activated by motor orienting for manual, though not saccadic, responses. Despite their functional independence therefore, temporal orienting and manual motor orienting nevertheless engage partially overlapping regions of left IPS, possibly reflecting their shared ontogenetic roots.



## Introduction

A soccer player receiving a pass uses information contained within the ball's trajectory to prepare both when the ball will reach him and with which part of his body (foot, chest, head) he will receive the pass. In the laboratory, it has repeatedly been shown that directing (or "orienting") attention towards the expected spatial location (Posner et al., 1980) or temporal onset (Niemi and Näätänen, 1981; Nobre, 2001) of an upcoming event (e.g., the ball's arrival) optimises responses to that event, as does selectively attending to the motor effector expected to execute the response (Rosenbaum, 1985; Rushworth et al., 2003).

While spatial orienting of attention has long been linked to right parietal cortex (Corbetta et al., 1993; Mesulam, 1981), both temporal (Coull and Nobre, 1998) and motor (Rushworth et al., 2003; Hesse et al., 2006) orienting of attention recruit similar regions of left parietal cortex. Neuroanatomical overlap in fronto-parietal circuits for spatial orienting and saccade preparation (e.g., Corbetta et al., 1998; Nobre et al., 2000) has been used to support the premotor theory of attention (Rizzolatti et al., 1994), which posits that (oculo)motor preparation for a spatially defined action guides the deployment of attentional resources in space. By analogy, preparation for a delayed action may also guide appropriate deployment of attentional resources in time. If so, the aforementioned neuroanatomical overlap in left parietal cortex for temporal and motor orienting could reflect their functional overlap. For example, preparation for action may induce a concomitant expectation of when that action is likely to be executed (Requin et al., 1991). Conversely (though not mutually exclusively), temporal expectation of an event's onset may automatically invoke (or "afford") preparation of a motor effector suitable for responding to that event (Gibson, 1979). We set out to determine whether it is possible to dissociate motor and temporal orienting, from both behavioural and neuroanatomical points of view. We predicted temporal orienting would benefit performance, and recruit left parietal cortex, even when the motor effector required to register the response was unpredictable.

Prior fMRI studies have used hand movements to measure performance benefits of temporal and motor orienting (Coull and Nobre, 1998; Rushworth et al., 2003) or predictability (Sakai et al., 2000). To test whether activation of left parietal cortex in these studies was specific to preparation of manual responses, we also

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examined temporal and motor orienting for saccadic eye movements. Prior behavioural studies have confirmed that temporal predictability can speed both smooth pursuit (de Hemptinne et al., 2007; Jarrett and Barnes, 2005) and saccadic eye movements (Bronstein and Kennard, 1987). Our mixed fMRI design allowed us to compare and contrast behavioural and neural correlates of temporal and motor orienting on hand versus eye movements within the same experimental paradigm. Moreover, we deliberately disentangled motor preparation from potential spatial confounds by using endogenous cues that did not allow preparation of a spatially selective response (e.g., left/right hand) but, rather, selective preparation of an entire effector system (ocular/manual) (see also Dickinson et al., 2003; Beurze et al., 2009). Both motor and temporal orienting could therefore be investigated independently of spatial orienting influences.

Finally, it should be noted that we have coined the terms "motor orienting" and "temporal orienting" deliberately in order to provide a direct analogy with the process of spatial orienting. With spatial orienting, attentional resources are directed to a specific location in space, with temporal orienting they are directed to a specific moment in time, while with motor orienting they are directed to a specific motor effector. The term motor orienting is thus equivalent to a selective form of motor preparation or motor intention. However, we prefer to retain our "orienting" terminology in order to make clear that similar attentional mechanisms can operate across different processing domains.

## Methods

A behavioural experiment was conducted before the scanning session to establish the validity of the experimental design, i.e., to evaluate the capacity of symbolic cues to induce attentional orienting independently along the motor and temporal dimensions.

### *Behavioural experiment*

#### *Subjects*

Fifteen subjects took part in the experiment (mean age 26 years; 6 females). All were healthy, with normal or corrected-to-normal vision. They were naïve as to the purpose of the study and gave informed consent. The study was performed in accordance with the ethical standards laid down in the Declaration of Helsinki (last modified 2004).

#### *Apparatus*

Subjects were seated in complete darkness on an ergonomic posture chair, with their head maintained straight ahead by a chin rest and a frontal support. They faced a 19″ LCD screen that presented visual stimuli at 60 Hz. A helmet-mounted infra-red sensor allowed recording of left eye position at 500 Hz (EyeLink II infra-red eye tracking system, SR Research, Mississauga, Ontario, Canada) with a spatial resolution of >0.1°. Precise measurements of horizontal and vertical eye position were achieved with a nine-point calibration grid. Saccade onsets were determined offline using data analysis programs implemented in Matlab (MathWorks, Natick, MA; multi-criterion detection using thresholds of velocity: 15 deg $s^{-1}$, acceleration: 3000 deg $s^{-2}$, and horizontal displacement: 1.5 deg). Button responses were recorded using a laboratory-made response box with two low trigger-force buttons that sampled manual responses at 1000 Hz. A real-time acquisition system (Keithley Instruments, Cleveland, OH) controlled the experiments using laboratory-made software (Docometre).

#### *Experimental procedure*

Subjects performed a choice-RT task. A background scene, comprising one central and two peripheral compound crosses (located ±10 deg horizontally from screen centre), was present throughout the task (Figs. 1B & C). The central cross acted as a place-marker for the presentation of cues and targets, while the peripheral crosses acted as response zones for lateral eye movements. Every trial had the same sequence of events. Trials started with central fixation for a variable period (600~800 ms). A visual cue was presented centrally for 100 ms. After one of two possible delays (ISI: 750 ms/ 1500 ms) a visual target was then presented centrally for 100 ms. Subjects were required to react to it as quickly as possible using one of two possible movements (hand/eye), which was indicated by the orientation of the target. A vertical target specified a hand movement (manual button-press) whereas a horizontal target specified an eye movement (oculomotor saccade). The laterality (left/right) of the response was determined by the horizontal black-to-white grating of the target, with subjects being required to respond on the side corresponding to the lighter side of the target. Therefore, subjects pressed a button placed under the index finger of the hand corresponding to the lighter side of vertical targets (for example see

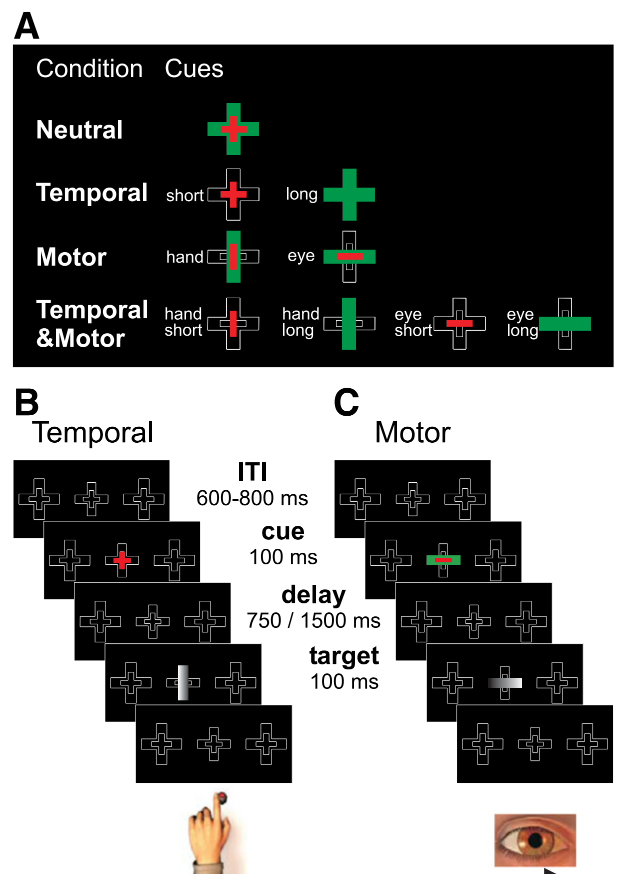


**Fig. 1.** Sequence of events in a trial. After a random inter-trial interval (ITI), a cue was presented centrally for 100 ms. After one of two possible delays (750/1500 ms), a target was presented centrally for 100 ms. The motor response to be given was indicated by the orientation of the target, with vertical targets specifying button-presses and horizontal targets specifying saccades. The laterality of the response was determined by target shading, such that subjects made left-/right-hand button-presses or left/rightward saccades to the lighter side of the target. A) The presence (+) or absence (−) of temporal (T) or motor (M) orienting cues were crossed in a 2×2 factorial design, yielding four cueing conditions: Temporal (T+M−), Motor (T−M+), Temporal&Motor (T+M+), Neutral (T−M−). Each of these conditions was associated with a specific set of centrally presented cues, which are illustrated here. B) Illustrative example of a trial in the 'Temporal' condition. The cue informed the subject that the target would appear after a short delay. After a short delay, the appearance of a vertical target with the lighter side on the left instructed the subject to produce a leftward manual response. C) Illustrative example of a trial in the 'Motor' condition. The cue informed the subject that the response to be produced would be a saccade. After a variable delay, the appearance of a horizontal target with the lighter side on the right instructed the subject to produce a rightward saccadic response. These are simply illustrative examples: all combinations of cue-type/delay/effector/side were presented.